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EXPERIMENTAL ANALYSIS OF THE ROLE OF SIBLINGS CALLS AFTER HATCHING IN CHICKS (*Gallus domesticus*): COMPARISON WITH AN ARTIFICIAL AUDITORY STIMULUS

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ABSTRACT: Several recent studies have emphasized the role of the maternal call in the attachment process in young nidifugous birds. Prenatal auditory stimulation (audition of sibling calls or self perception) is a determinant factor in the development of the attractiveness of the maternal assembly call. However, little is known about the role of sibling calls after hatching. In particular, they may be involved in attraction between broodmates and, in this way, they may compete with the maternal call during the development of attachment. These experiments were designed to test the value of postnatal audition of sibling calls (C). Several groups of chicks were placed in an operant conditioning paradigm in which the instrumental response allowed the birds to receive either auditory, visual or audiovisual stimuli. Results demonstrated that audition of sibling calls is appetitive but, surprisingly, the chicks did not evince a clear-cut choice for this stimulus over audition of a pure tone (T). Moreover, chicks were tested in a choice situation between two audiovisual stimuli. The visual stimulus was the vision of their own image in a mirror (V). In this choice situation between "V+C" and "V+T," chicks did not choose the "V+C" stimulus significantly more. Thus, these data, without denying communicative value to sibling calls, support the hypothesis that they do not play an important role in attraction between broodmates and that the main effect of their audition is an activating one.

RÉSUMÉ: Chez le jeune nidifuge, le rôle du gloussement maternel dans le processus d'attachement filial est bien connu. Plusieurs études récentes ont montré que les stimulations auditives survenant durant la période prénatale (autoperception et audition des cris des autres embryons) constituent un élément déterminant dans le développement du caractère attractif de ce gloussement. Peu de choses, cependant, sont connues sur le rôle des cris des autres jeunes après l'éclosion. En particulier, il pourraient être impliqués dans les processus d'interattraction entre les jeunes d'une même couvée. Ceci pourrait donc les faire entrer en compétition avec le cri maternel au cours du développement de l'attachement filial. Ces expériences ont été construites dans le but d'étudier la valeur de ces cris après l'éclosion. Plusieurs groupes de poussins ont donc été placés dans une procédure de conditionnement opérant dans laquelle la réponse instrumentale permettait aux sujets d'obtenir, selon les cas, un stimulus visuel, un stimulus auditif ou encore un stimulus audiovisuel.

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Les résultats font apparaître que l'audition des cris de poussins (C) constitue un stimulus appétitif mais que, de manière surprenante, les sujets n'effectuent pas de choix net entre ce stimulus et l'audition d'un son pur (T). Les poussins ont également été testés dans une situation de choix entre deux stimuli audiovisuels. Le stimulus visuel consistait en la présentation de l'image de l'oiseau dans un miroir (V). De nouveau, lorsqu'ils sont placés dans une situation leur permettant d'obtenir soit "V+C" soit "V+T," les sujets n'effectuent pas de choix net. Sans nier toute valeur de communication aux cris des autres jeunes, ces résultats tendent à conforter l'hypothèse selon laquelle ces cris ne jouent pas un rôle important dans l'interattraction entre jeunes d'une même couvée. Leur rôle pourrait, en fait, être essentiellement un rôle activateur.

In young nidifugous birds, hearing the maternal call induces approach responses towards the sound source. These postnatal locomotor responses are partly dependent upon events occurring during late embryogenesis. Thus, several studies have shown the importance of embryonic auditory experience (self perception or audition of sibling calls) upon the development of responsiveness to maternal assembly calls (Gottlieb, 1975a,b,c, 1979, 1981).

Prenatal learning may also impede spontaneous auditory preferences and, thus, postnatal locomotor responses. For example, I have shown, in a previous experiment, that chicks placed in a choice situation between two pure tones (500 Hz and 1000 Hz) also spontaneously prefer the low-frequency tone. Such a spontaneous preference for low-frequency sounds has been demonstrated by other authors (Fischer, 1972; Gray & Rubel, 1981). But pairing prenatal audition of the 1000 Hz tone with pertinent modifications of the embryo's environment (such as warming and egg-rotation) significantly delayed the expression of such a preference (Delsaut, 1991).

During this late embryogenesis period, embryos emit several types of calls including as many "distress calls" as "pleasure calls" (Guyomarc'h, 1972). Some vocal interactions between the hen and the embryos also take place during this period. Such interactions mainly occur when the hen comes back to the nest and turns over her eggs (Guyomarc'h, 1974a,b; Tuculescu & Griswold, 1983). Thus, both maternal and sibling calls are likely to be associated with warming and egg-rotation. In this way, prenatal learning is likely to contribute to the maternal call attractiveness ontogenesis, but the same process may also confer an attractive value on some of the sibling calls. Such a process would thus lead to these two types of calls competing after hatching.

The purpose of this study is to test the value of postnatal audition of sibling calls.

GENERAL METHODS

Animals

The 169 battery-reared chicks (*Gallus domesticus*) used in the nine experiments in this report were of the viandotte breed and were obtained

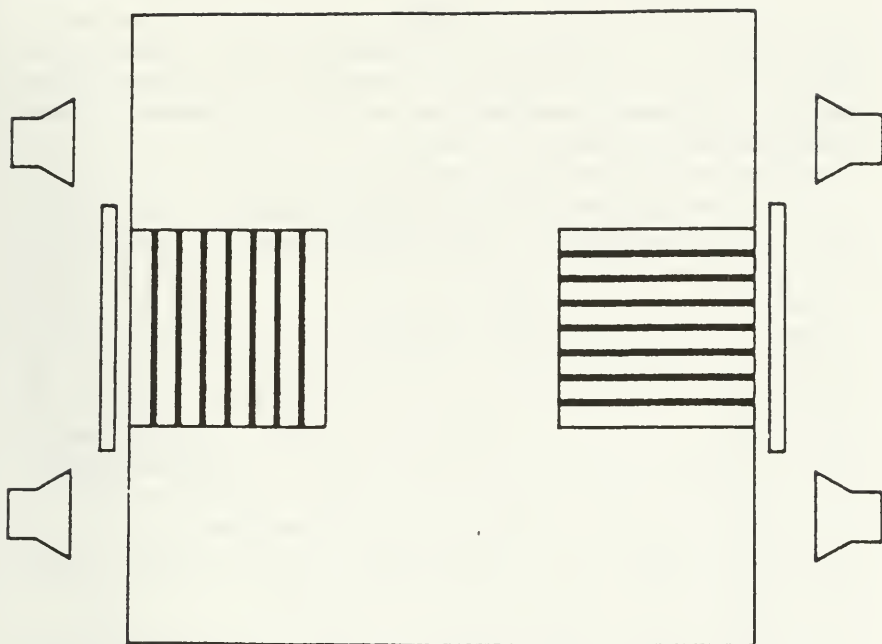


FIGURE 1. Diagram of the experimental cage. One-way mirrors are symbolised by the two narrow rectangles, loudspeakers by the four polygonal figures and active zones by the two hatched squares.

from a single supplier. In order to detect an eventual effect of age, each group was divided into two sub-groups. Chicks were thus tested either just after they had been removed from the incubator (neonate birds = N, 20 hours of age \pm 4 hours) or at six days (one week birds = W, 140 hours of age \pm 4 hours). Between experimental sessions, chicks of each group were kept together in a breeding cage (60 \times 60 \times 120 cm) in a room continuously warm (28 °C). In this way, they were always in visual and auditory contact. Food and water were available *ad libitum*.

Apparatus and Test Situation

The experimental apparatus has been described elsewhere (Delsaut, 1991). Briefly, experiments were run in a testing cage (40 \times 40 \times 40 cm). Photocells, regularly set along two adjacent sides of the cage, enabled us to follow the chicks' movements. The individual's mean position, computed once a second by microprocessor (Apple IIe), was displayed on a monitor. Two "active" zones (12.4 \times 12.4 cm), which were near two opposite walls, were marked out on the floor of the cage with hatchings (Fig. 1). The operant response (passing over these zones) triggered stimuli, which were presented for a maximum of 20 sec or were stopped as

soon as the bird left the active zone. These time conditions were used in all the experiments reported here. In order to get the stimulus again, chicks had to go out of the active zone before coming back in. In four experimental situations, passing over one of these two zones triggered no stimulus (control zone).

Four sorts of stimuli were used in these experiments:

1. A "natural" auditory stimulus which consisted of a recorded sequence of calls produced by a nondisturbed, active group of eight chicks (C). The recorded sequence lasted 90 sec and was recorded on a tape loop (intensity: from 75 to 80 dB, depending on the position in the cage).

2. An artificial auditory stimulus, which was a sinusoidal pure tone (T) of 1000 Hz, of 200 msec duration, repeated every three seconds at the same intensity as C (from 75 to 80 dB, depending on the position in the cage). This tone was not in the frequency range known to be spontaneously attractive to nidifugous neonates. Other characteristics (duration, rhythm) did not obviously match those of natural specific calls (Gardahaut, Guyomarc'h, & Fenaux, 1982; Collias, 1987).

Both auditory stimuli were broadcast from a Revox A77. Sound levels were measured with a Brüel and Kjaer (type 2226).

3. The bird's own image (V) in a one-way mirror (15×15 cm).

4. A light stimulus (L) which consisted of lighted electric bulbs behind a frosted glass window (15×15 cm). In this condition, as with V, a ventilation system minimized the temperature variations behind the glass.

Test Procedure

Prior to testing, each chick was marked on the top of its head with a marking pen so that it could be rapidly identified. The subject was placed at the centre of the experimental cage three times a day for two days. At the first two daily sessions, their ages were respectively 20 and 44 h (± 4 h) for N chicks and 140 and 164 h (± 4 h) for W chicks. Each experimental session lasted 15 min (900 sec) and the chick was returned to its breeding cage at the end of the session. To minimize the effects of cyclical variation of activity, the experimental sessions took place at different times of the day with three h ($\pm \frac{1}{2}$ h) between two consecutive sessions.

In accordance with the conditions, there were one or two active zones but these two zones, active or not, were always marked out on the floor. In order to test for possible positional biases the active zone(s) was/were reversed for each half-group of chicks.

Two parameters were recorded: the time spent on each hatched zone, and activity, which was evaluated as the number of operant responses. Number and duration of passings over each zone were compared using a Student *t* test.

Each zone was identified by the stimulus it provided access to (for

TABLE 1
Experimental Situations.

Experiment 2 was Divided into Two Parts: 2₁ and 2₂. According to the Experimental Situation, there were either One or Two (*) Active Zones and Passing over each Zone Triggered No Stimulus, One Stimulus or the Simultaneous Presentation of Two Stimuli. Stimuli are Identified by the Following Letters: C, T, V, L, O (See General Methods). Number of Chicks: N = Neonates, W = Week Old Birds

<i>Experiments</i>					
<i>1</i>		<i>2₁</i>		<i>2₂</i>	
1a		2a		2d*	
C vs O		V vs O		V + C vs V	
N = 10	W = 10	N = 7	W = 7	N = 9	W = 7
1b		2b		2e*	
T vs O		L vs O		V + T vs V	
N = 11	W = 10	N = 10	W = 10	N = 9	W = 9
1c*		2c*		2f*	
C vs T		V vs L		V + C vs V + T	
N = 10	W = 10	N = 10	W = 8	N = 11	W = 11

example: T for the artificial tone, V+T for the simultaneous presentation of the bird's own image and the artificial tone, O for the control zone).

Experimental situations are summarized in Table 1.

EXPERIMENT 1

The present study was designed to test, in an operant conditioning paradigm, the effect of the audition of C on isolate chicks. The eventual effect of C may be related to the perception of some specific features, but it may also depend upon a more general effect of the auditory stimulation. With this in mind, the effectiveness of C was compared with that of an artificial auditory stimulus (T). As stated above, T was not in the frequency range known to be spontaneously attractive and other physical characteristics did not obviously match those of natural calls.

Results

Data are summarized in Figure 2 and Table 2.

Experiment 1a: Appetitive Value of C. The two groups of chicks spent significantly more time on the C zone (N chicks: $t = 2.44$, $p < .05$; W chicks: $t = 2.43$, $p < .05$). Activity was also higher on the active zone

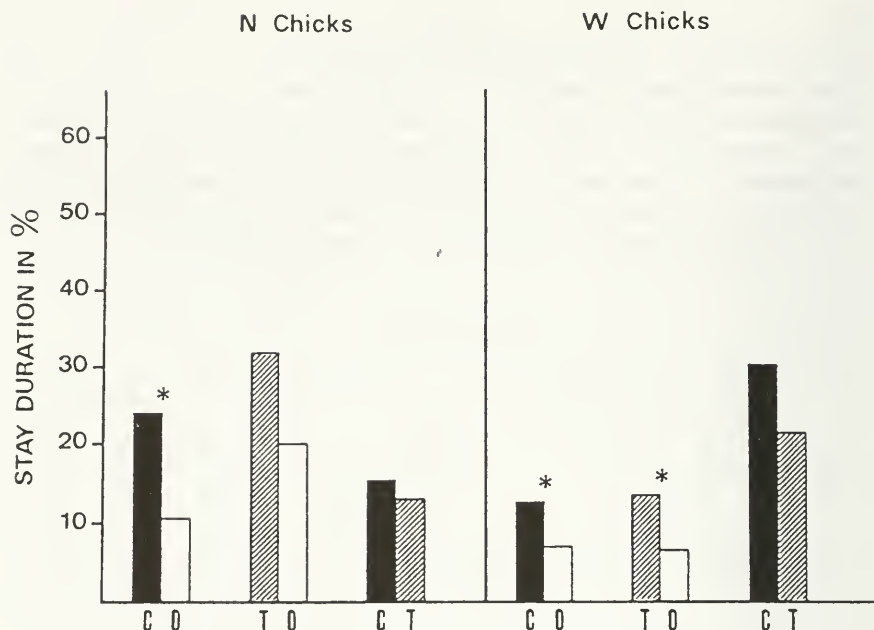


FIGURE 2. Appetitive values of the auditory stimuli. Histograms show the mean time spent in each zone in the three choice conditions (as a percentage of the total duration of a session). * = statistically significant difference. C = audition of recorded calls of a nondisturbed, active group of chicks. T = audition of a pure tone (1000 Hz). O = no stimulus.

for the two groups and the differences were significant (N chicks: $t = 4.96$, $p < .001$; W chicks: $t = 4.74$, $p < .01$).

Experiment 1b: Appetitive Value of T. The chicks also exhibited a preference for the T zone in this condition. According to the group considered, this trend was significant either for the time spent in the active zone (N chicks: $t = 1.246$, NS; W chicks: $t = 3.02$, $p < .02$) or for activity (N chicks: $t = 2.69$, $p < .05$; W chicks: $t = 1.45$, NS).

Experiment 1c: Comparison of the Appetitive Values of C and T. The chicks did not choose between C and T when these stimuli were concurrently presented (duration: N chicks: $t = 0.32$, NS; W chicks: $t = 1.05$, NS; activity: N chicks: $t = 0.068$, NS; W chicks: $t = 1.89$, NS).

Discussion

Experiment 1a showed that audition of the C stimulus is an appetitive stimulus for an isolate chick. Much less expected was the finding that a pure tone played back repetitively also appeared to be appetitive. Furthermore, neither N chicks nor W chicks chose C or T more than the other.

TABLE 2

Mean Number of Passings over the Two Hatched Zones for all Chicks in each Experimental Situation

		<i>C</i>	<i>O</i>	<i>T</i>	<i>O</i>	<i>C</i>	<i>T</i>
Experiment 1	N	8.5	5.5	9.8	7.0	4.7	4.3
	W	12.6	7.0	7.2	5.9	28.6	24.0
		<i>V</i>	<i>O</i>	<i>L</i>	<i>O</i>	<i>V</i>	<i>L</i>
Experiment 2 Part 1	N	6.8	3.8	29.8	20.8	5.5	2.1
	W	26.2	16.3	20.8	16.5	19.0	7.3
		<i>V+C</i>	<i>V</i>	<i>V+T</i>	<i>V</i>	<i>V+C</i>	<i>V+T</i>
Experiment 2 Part 2	N	7.0	5.5	9.4	8.0	4.0	4.1
	W	15.2	12.2	5.4	5.3	16.4	17.5

EXPERIMENT 2

An audiovisual stimulus is a more attractive and a more effective imprinting stimulus than a visual one alone. Moreover, pairing an auditory stimulus with the visual imprinting stimulus may contribute to the process that allows individual maternal call discrimination by the neonate (Evans, 1972, 1975, 1977; Evans & Mattson, 1972; Cowan, 1973, 1974a,b; Cowan & Evans, 1974). In the experimental conditions used above, auditory stimuli were artificially dissociated from visual ones. The lack of obviously oriented behaviour in Experiment 1c may thus be linked to such conditions.

The following experiments were designed to test the effect of pairing either sibling calls or the T tone with a visual stimulus. In the experimental conditions designed here, the chicks were given the opportunity to see their own images.

This experimental series was divided into two parts. In the first, a control experiment, the effectiveness of the chick's own image in a mirror in the paradigm used here was tested. After that, the effect of pairing visual to auditory stimuli was evaluated.

PART 1: APPETITIVE VALUE OF THE CHICK'S OWN IMAGE IN A MIRROR

Gallup, Montevicchi, and Swanson (1972) have shown that mirror-image stimulation is an appetitive stimulus and that it is more effective in reducing distress calls in isolate chicks when compared with visual access to a living congener. In this way, it may be considered a super-normal stimulus. But mirror-image stimulation also elicits aggressive

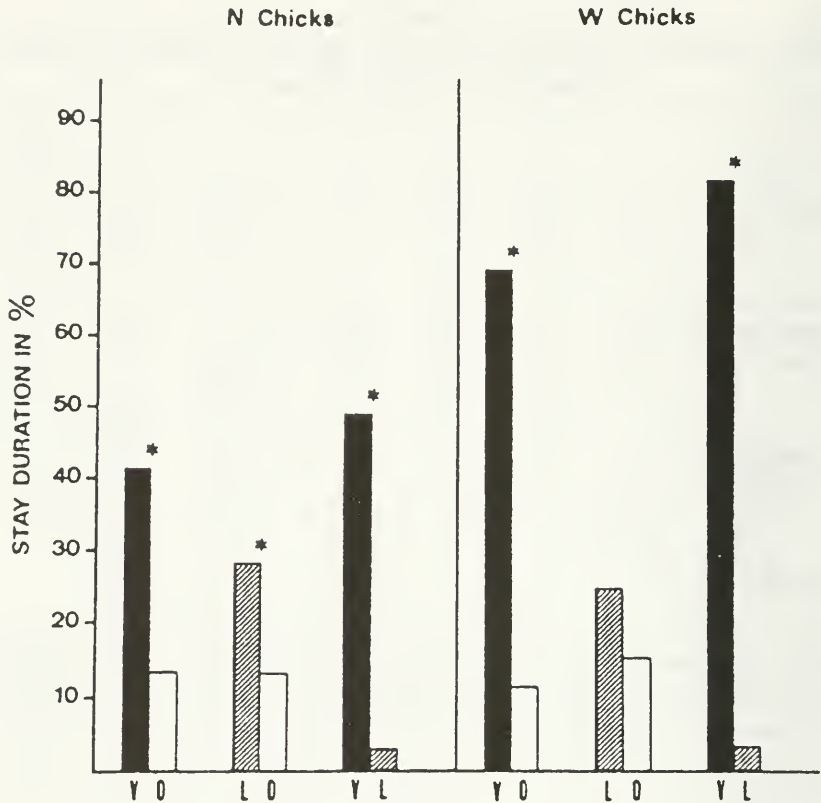


FIGURE 3. Appetitive values of the visual stimuli. Histograms show the mean time spent in each zone in the three choice conditions (as a percentage of the total duration of a session). * = statistically significant difference. V = presentation of the chick's own image in a mirror. L = variation of luminosity behind a frosted glass. O = no stimulus.

behaviour. This experiment was, therefore, designed to confirm the appetitive value of the chick's own image in a mirror (V) in the particular experimental conditions used here.

Appearance of V was accompanied by a variation of luminosity which is known to be reinforcing (Meyer, 1968). V was thus compared in the same experimental conditions with a stimulus that varied in luminosity (L) in order to ensure that its appetitive value was linked to the presence of specific stimuli.

Results and Discussion

Data are summarized in Figure 3 and Table 2.

Experiment 2a: Appetitive Value of the Chick's Own Image. Neonates as well as week-old birds spent significantly more time in the V zone than in the O zone (N chicks: $t = 3.39$, $p < .02$; W chicks:

$t = 9.02, p < .001$). Activity was also significantly oriented towards the V zone (N chicks: $t = 4.88, p < .01$; W chicks: $t = 4.93, p < .01$).

Experiment 2b: Appetitive Value of a Light Stimulus. The onset of a light stimulus was appetitive for N chicks. Tendencies were not significant for W birds (duration: N chicks: $t = 3.35, p < .01$; W chicks: $t = 1.81, NS$; activity: N chicks: $t = 4.20, p < .01$; W chicks: $t = 1.89, NS$).

Experiment 2c: Comparison of the Respective Appetitive Values of V and L. For both groups of chicks used in this experiment, the V stimulus appeared more appetitive than the L (duration: N chicks: $t = 5.46, p < .01$; W chicks: $t = 26.68, p < .001$; activity: N chicks: $t = 2.62, p < .05$; W chicks: $t = 6.37, p < .001$).

Discussion

This experiment confirms the appetitive value of the bird's mirror-image. This was consistent with other results obtained in adult birds (Thompson, 1964; Delsaut & Roy, 1980a,b). It is also known that a visual imprinting stimulus is positively reinforcing (Peterson, 1960; Campbell & Pickleman, 1961; Bateson & Reese, 1969; Hoffman, Stratton, Newby, & Barrett, 1970; Simner, 1975). According to the results of Experiments 2b and 2c it can be assumed that, in these experimental conditions, the mirror-image exposes the bird to social stimuli which are highly appetitive.

PART 2: APPETITIVE VALUE OF AN AUDIOVISUAL STIMULUS

This experiment was designed to test the influence of the bird's own image upon the appetitive value of the two auditory stimuli. For this purpose two different audiovisual stimuli (V + C and V + T) were compared with V or with each other.

Experiment 2d: Comparison of the Appetitive Value of V + C with the Appetitive Value of V. N chicks as well as W chicks do in fact discriminate between these two stimuli and both the number of passings over and the time spent on the V + C zone were significantly higher than on V (duration: N chicks: $t = 2.48, p < .05$; W chicks: $t = 5.47, p < .01$; activity: N chicks: $t = 2.36, p < .05$; W chicks: $t = 3.44, p < .02$).

Experiment 2e: Comparison of the Appetitive Value of V + T with the Appetitive Value of V. Only W chicks spent more time on the V + T zone and this trend was significant. N chicks did not show any trend towards either of them (duration: N chicks: $t = 0.02, NS$; W chicks: $t = 2.38, p < .05$; activity: N chicks: $t = 2.0, NS$; W chicks: $t = 0.49, NS$).

Experiment 2f: Comparison of the Appetitive Value of the two Composite Stimuli, V + C and V + T. Neither N chicks nor W chicks oriented their behaviour towards either of the two active zones (duration:

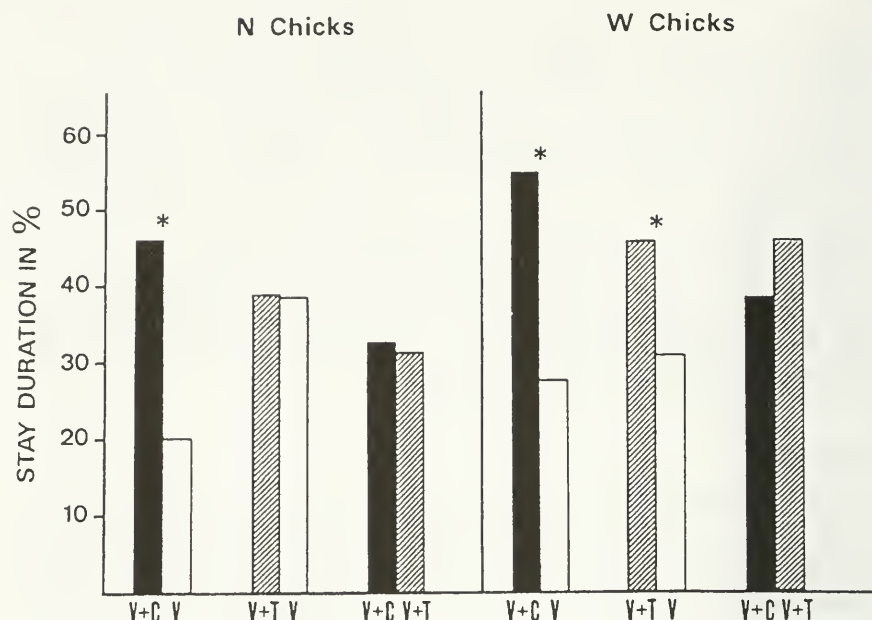


FIGURE 4. Appetitive values of the audiovisual stimuli. Histograms show the mean time spent in each zone in the three choice conditions (as a percentage of the total duration of a session). * = statistically significant difference. V + C = simultaneous presentation of the bird's own image in a mirror and of recorded sibling calls. V + T = simultaneous presentation of the bird's own image in a mirror and of a pure tone (1000 Hz) played back repetitively.

N chicks: $t = 0.15$, NS; W chicks: $t = 1.05$, NS; activity: N chicks: $t = 0.71$, NS; W chicks: $t = 0.73$, NS).

Discussion

The composite stimulus V + C is a more appetitive stimulus than V alone. The V + T stimulus did not obviously appear to be more pertinent than the V. Thus, the weak value of the T stimulus detected in Experiment 1b seemed to be masked by the strong appetitive value of V. However, convergent with the result of Experiment 1c was the lack of choice between the V + C and the V + T association.

GENERAL DISCUSSION

The first experiment confirmed that audition of sibling calls is an appetitive stimulus for an isolate chick. This might be expected, owing to its importance during embryogenesis. Conversely, much less expected was the demonstration of the appetitive value of the artificial auditory stimulus and the surprising lack of differentiation between C and T.

Results of the second experiment corroborate the lack of choice between the "natural" and the "artificial" auditory stimuli. It has been demonstrated in other contexts that an audiovisual stimulus is more attractive and more appetitive than a visual one. This is true in young nidifugous (Brown, 1975; Ewing, Ewing, & Vanderweele, 1975) and the influence of auditory stimulation has been interpreted in terms of arousal (Brown, 1977). The preference for the audiovisual stimulus is true also in adult non-nidifugous birds (Delsaut & Roy, 1980a,b).

Such an effect is confirmed here, at least for V+C which appears to be a more appetitive stimulus than V alone. But, again, chicks did not choose between V+C and V+T. On the whole, the 42 chicks of both age groups used in Experiments 1c and 2f did not evince a significant choice, the preference being measured either by time spent on the active zone or by activity.

It must be recalled that, in all the experiments described here, chicks were socially reared and then tested individually. In another context, results reported by Blaich, Miller and Hicinbothom (1989) and by Lickliter and Gottlieb (1986) suggest that such differences in social experience, between the training and the testing situations, interfere with maternal imprinting. But Dyer and Gottlieb (1990) demonstrated that this was not due to the social contextual difference between these two situations. Moreover, despite the fact that visual and auditory stimuli cannot be directly compared, it must be noted that, here, in the same conditions, chicks evince a clear-cut preference for the "natural" stimulus (V) and not for C. This procedural detail does not, therefore, appear to be crucial.

These results thus provide grounds for questioning the role of sibling calls in the attraction between broodmates.

In another context, Gaioni (1982, 1987), Gaioni and Platte (1982) and Gaioni, Applebaum, and Goldsmith (1983) have shown that two isolated ducklings alternate their distress calls. It is a common assertion that young birds ignore the distress calls of siblings. According to Gaioni (1982), alternation shows that ducklings are highly sensitive to these calls. Functionally, alternation could increase maternal retrieval. This interpretation has been contested by Lamprecht (1985, 1987) who remarks that the phenomenon has never been observed in natural conditions. Moreover, his own data show that goslings alternate their distress calls significantly more often with an artificial tone. Thus, alternation might not be the result of a cooperative action.

Without denying communicative value to sibling calls, the results presented here provide grounds for asking whether their effect is not mainly activating. In that case, without competing with the maternal calls, sibling calls might make the activity level of the sibs more similar and thus contribute to preserving group cohesion.

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EFFECTS OF PHYSICAL ENVIRONMENT AND SOCIAL EXPERIENCE ON STIMULUS SEEKING BEHAVIOR AND EMOTIONALITY IN RATS (*Rattus norvegicus*)

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ABSTRACT: The influences of the physical and social aspects of the environment on temperament in rats are reported in two experiments. In Experiment One changes in animal behavior due to social isolation and enrichment of the physical environment were studied in rats subjected to experimental conditions when they were 25–30 days old. Enrichment of the physical environment led to decreased need for light stimulation and increased exploratory behavior. Social isolation led to an increase in emotional reactivity. Experiment Two was analogous to Experiment One, differing only in that 60–70 day-old animals were given the experimental conditions. In this case enriched physical environment and social isolation led to decreased exploratory behavior. Need for light stimulation was affected by the interaction of experimental variables. Need for kinesthetic and tactile stimulation were affected by the social environment. Enrichment of the physical environment also led to a decrease in emotional reactivity in the rats. Our experiments indicate that environmental effects were age-contingent. It is proposed that there is probably a relationship between categories of environment and temperament. Further, our findings draw attention to the possibility of a related evolution of sensory systems and temperamental traits.

Such temperamental features of humans and animals as need for sensory stimulation or emotional reactivity have been considered to be strongly determined by genetic factors (Strelau, 1983). However, several theoretical approaches have postulated that temperamental features can respond to environmental influence (Denenberg, 1964; Strelau, 1983; Matysiak, 1985). Active self-exposure by animals to sensory stimulation in specially constructed chambers (Wong, 1976; Matysiak, 1985) as well as running in a running wheel can be assumed to indicate need for sensory

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stimulation (Matysiak, 1985). Archer (1973) and Walsh and Cummins (1976), in turn, have shown that behavior in open field tests is a valid (with some limitations) indicator of widely-conceptualized emotionality and exploration in animals. Brush et al. (1985) have shown speed of acquisition of defensive responses to be a valid measure of emotional reactivity in animals.

Manipulating the so-called social environment of animals is frequently used in studies of the effects of environmental factors on temperament. Koch and Arnold (1972) found increased emotional reactivity in rats, as measured by heart rate and open field defecation and urination, in response to limitation of the animal's contact with the mother in early stages of development. Socially deprived rats also revealed less exploratory behavior than control animals.

The most marked effects of social isolation on exploratory behavior in rats have been found when isolation was introduced between the twenty-fourth and forty-fifth day of life. Rats isolated from their peers at that age revealed increased exploration of an object but were more reluctant to explore a new cage (Einson & Morgan, 1976). Baenninger (1967) found that the period between 16–20 and 35–40 days of life is a time of intensive peer play in rats. Marked changes in animal behavior due to social isolation during this period suggest that it is a critical period for social behavior and emotionality (Einson & Morgan, 1976).

Isolation at a later age also affects exploratory behavior in rats (Renner & Rosenzweig, 1986) and the observed changes in behavior are of mainly qualitative, not quantitative, nature. Renner (1987) found that socially isolated rats had a scantier repertoire of exploratory behavior and such behavior was of a generally lower level as compared with animals maintained in an enriched environment.

Studies by Parker and Morinan (1986) support the view that isolated rats are more anxious than rats maintained in a group. Isolated animals showed a lower level of exploratory behavior and higher emotional reactivity.

A frequent manipulation of the physical environment in rat studies consists of enriching the environment. However, Renner (1987) and Renner and Rosenzweig (1986) found that the effects of enrichment can be observed throughout the life of the rat. Forgy and Michelson-Read (1962) showed that the most important period for acquisition of experience in an enriched environment is the period between the twenty-second and forty-third day of life.

Sackett (1967) found that sensory experience in the early stages of life in rats affects preference for specific modalities of stimulation. Sensorially deprived rats preferred less complex and less novel stimuli. Greatest exploratory behavior, on the other hand, was found in animals maintained in standard conditions as regards degree of stimulation.

Smith (1972) analyzed open field behavior (exploration) in rats main-

tained in an enriched as opposed to a deprived environment. A second variable controlled in their study was richness of environment prior to or after weaning. Exploration in the open field was affected by environmental richness irrespective of the developmental stage of animals exposed to experimental treatment. Animals maintained in deprived conditions explored more than animals maintained in enriched conditions.

Manosevitz (1970) compared the behavior of mice maintained in standard and enriched environments using the open field test, activity wheel, and competition for food as dependent variables. Mice maintained in the enriched environment were more active in the open field and in the activity wheel than mice maintained in the standard conditions. The former were also less reactive emotionally and were quicker to learn to acquire food when it was scarce.

Hennessy, Hershberger, Bell, and Zachman (1976) and Tees, Midgley, and Bruinsma (1980) found that rats reared early in life in an environment enriched in sensory stimulation select environments that are more stimulating.

Changes in behavior due to experience in an enriched environment seem to be most conspicuous when the rat explores an object (Renner & Rosenzweig, 1986; Renner, 1987). These authors suggest that the elementary forms of exploration, i.e., emotional reactivity and general motor activity, are much less affected by environmental manipulations than complex activities.

The work reviewed above leads to the hypothesis that social and physical environmental factors are important determinants of behavior aimed at securing sensory stimulation.

Matysiak and Toeplitz (1990) studied the effect of genetic and environmental factors on the need for stimulation and found that rats maintained in an enriched environment show reduced need for light stimulation. Need for kinesthetic and tactile stimulation was not affected by environmental factors. However, this finding was not confirmed by the next work by Matysiak, Ostaszewski, Pisula, and Watras (1992). It was argued that the lack of corroboration could be due to insufficient control of the age of the studied animals in the Matysiak et al. (1992) study.

The following experiments were undertaken to test the effects of environmental factors on need for stimulation and emotional reactivity, and the relevance of age at the time of treatment. Since in many of the studies reported in the literature (Renner & Rosenzweig, 1986; Renner, 1987; Matysiak et al., 1992) environmental (in the sense of physical) and social factors are confounded, social isolation and enrichment of the physical environment were treated as two independent experimental variables in the present study. The main purpose of this study was to estimate the relative role of physical and social influences on temperamental characteristics in rats.

Four tests were used in both experiments:

1) a chamber for self-exposure to light stimuli, to measure the level of need for light stimulation,

2) a modified dual activity wheel to measure the need for kinesthetic and tactile stimulation and to measure preference for mobile activity supplying poor (kinesthetic and tactile) or rich (kinesthetic, tactile, and light) stimulation,

3) an open field test to investigate emotionality and exploratory behavior,

4) a standard shuttle-box to measure emotional reactivity during avoidance-response training.

All animals used in both experiments came from the same colony at the same time.

EXPERIMENT ONE

In this experiment a 2×2 factorial design was adopted with maintenance in an enriched versus a standard condition as one factor and in a group versus in isolation as the second factor. The rats were 25–30 days old at the start of the experiment.

Animals

Forty-eight outbred male Wistar rats were observed. The animals came from an animal dealer's colony about 40 kilometers from our laboratory. They were weaned when about 25 days old. Once weaned the rats were transported to our laboratory.

Apparatus

Two types of maintenance cages were used: a standard wire cage, $40 \times 30 \times 20$ cm, and an "enriched" wire cage twice as large ($40 \times 60 \times 20$ cm) and equipped with a swing (15.5 cm from top, 8.5 cm in width), a see-saw (20×5 cm, 7 cm high in the middle point), a ladder (21×11 cm, 0.7 cm between rungs), and two table-tennis balls. All equipment (but balls) were made of metal.

The chambers for self-exposure to light stimuli ($40 \times 30 \times 20$ cm) have been described elsewhere (Matysiak, 1985). As the base for constructing them, we used the maintenance cages. Inside, on the two opposite longer walls, 10 cm above the base, were symmetrical bars. Pressing on one bar (experimental) switched on a light of 1.6 lux for the duration of the bar press whereas nothing happened when the other bar (control) was pressed. The source of light was nine small (10 Watts) bulbs mounted at the cover of the chamber behind frosted glass. The number of bar presses and their duration were registered using the MS IMPOL computer system.

The activity wheels were in similar cages as the chambers for self-exposure of light. The base of the chamber was the maintenance cage. On two opposite, shorter walls were doors leading to the activity wheels. These doors remained open all the time. Both wheels were identical and consisted of a wire running track 15 cm wide and 30 cm in diameter. Both wheels had identical inertia (the same weight, construction and the same time and number of free rotations during the testing trials). They differed as to effects of movement. Movement sufficient to rotate the experimental wheel 10° switched on a light in the whole chamber for the duration of the movement plus three seconds. The 3 sec delay in switching off the light was introduced in order to counteract any flickers due to slight, uncontrolled movements of the wheel (e.g., directly after the animal had left it). Moving the control wheel had no additional effects. The number of revolutions of the experimental and control wheels were recorded. In this test, as in the previous one, water and food were available *ad libitum*.

The circular open field, 160 cm in diameter, was surrounded by a white, metal wall 35 cm high. The floor was made of white plastic tiles size 20 × 20 cm. In the center, 120 cm above the floor, a 200 W bulb was suspended.

The shuttle box for training the avoidance response was 48 × 22 × 23 cm large and was built on a base of metal rungs 3 mm thick and placed 14 mm apart. The walls of the chambers were made of Plexiglas tiles of which three were coated in light-absorbent material while one was uncoated and permitted observation of the animal. The conditioned stimulus, a light of 5 lux, was supplied by bulbs secured in the lid of the chamber behind frosted glass. The unconditioned stimulus was an electric shock issued through the floor bars.

Procedure

One day after arrival at the laboratory the rats were transferred to their home cages. Twelve rats were placed, 6 each, in two standard cages and twelve were placed one each in 12 standard cages, 12 additional animals were placed six each in two enriched cages and the final 12 were placed one each in 12 enriched cages. A temperature of 23 °C and a 12 h light/dark cycle (beginning at 0800 h) were used in the maintenance room.

When the rats were about 90 days old the experiment proper began. All animals were first tested in the self-exposure to light chamber and in the activity wheels (23.5 h tests). The order of testing of each animal and the order of tests were randomized. Each animal took the two tests on two consecutive days. Each test started at 1230 h.

Previous research (Matysiak, 1985; Matysiak & Toeplitz, 1990) has shown that when animals are tested in the light self-exposure chamber

most information is gained when the indices of two basic variables are analyzed: need for stimulation and general motor activity.

1) Need for stimulation was measured using the following formula:

$$NS = Ne/(Ne + Nc) \times Te/(Te + Tc)$$

where

Ne = Number of presses on experimental bar

Nc = Number of presses on control bar

Te = Total duration of experimental bar depression

Tc = Total duration of control bar depression

2) General motor activity was measured by computing the total number of presses on both bars.

General motor activity index and the number of wheel rotations were analyzed for the initial 90-min phase of measurement.

Both the above indices and NS coefficient were analyzed for a 22-hour phase following the initial phase.

Two days after all rats completed the tests they were observed in the 3 min open field test. The number of defecations, urinations, crossed squares and rearings were recorded.

The last test was the conditioning of the defensive responses. Within two days each animal went through twenty trials in two sessions, ten trials per session. The strength of the shock was adjusted individually and ranged from 1.5 to 2.5 mA. The conditioned stimulus lasted 4 sec after which the shock was introduced. The electric current and the light were switched off when the rat responded correctly, i.e., crossed a 3 cm barrier running across the middle of the cage. The following indices were measured: duration of escape, i.e., the time that elapsed from the moment the electric current was switched on until the animal switched it off; the duration of avoidance, i.e., the time that elapsed from the moment the light was switched on till the animal crossed to the opposite side of the cage before the electric shock was turned on, and the number of correct avoidance responses.

RESULTS

Two-factor ANOVA with physical environment and social environment as factors was carried out. In the occurrence of interaction, simple effects were tested with Fisher's procedure.

Animal Behavior in Self-exposure Chamber and Activity Wheels during the First 90 Min Phase of Measurement. During the initial 90-min phase of measurement, the only behavior that differentiated the animals from the different groups was activity in the light wheel, $F(1,43) = 4.569$, $p = .039$ (Figure 1a). This was the main effect of the physical environment. Rats maintained in the enriched environment ran in this wheel more than rats maintained in the standard environment.

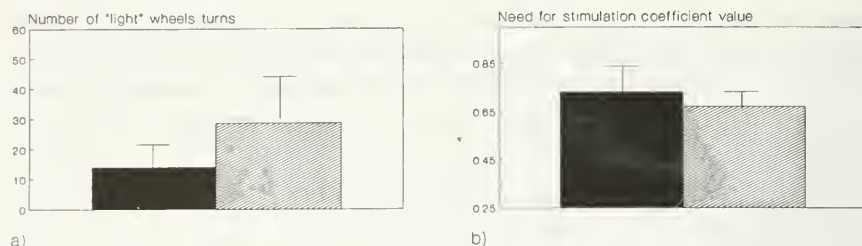


FIGURE 1. Means and standard deviations of: a) number of light wheels turns during first 90 min of measurement, ■ standard, ▨ enriched; b) need for stimulation coefficient [$NS = Ne/(Ne + Nc)$] computed on the base of results of the second 22 h of measurement, ■ standard, ▨ enriched.

There were no differences for the control wheel.

Animal Behavior in Self-exposure Chamber and Activity Wheels during the 22 H Test Period. The index computed according to the complete formula showed no differences but the analysis of variance of the partial index of need for stimulation [$NS = Ne/(Ne + Nc)$] revealed a higher need for light stimulation in the animals maintained in a standard environment as compared with the animals maintained in the enriched conditions, $F(1,32) = 6.232$, $p = .018$ (Figure 1b).

No differences among groups were found for all behavior measures in the activity wheels.

Open Field Behavior. The animals differed in the number of rearings. An interaction of physical and social factors was found, $F(1,43) = 4.42$, $p = .042$ (Figure 2a). Socially isolated rats maintained in the enriched environment reared more than socially isolated rats maintained in standard conditions.

Socially isolated animals urinated more than animals maintained in groups, $F(1,35) = 6.784$, $p = .014$ (Figure 2b).

Acquisition of Defensive Response. Rats maintained in isolation made less correct avoidance responses than group maintained rats, $F(1,33) = 13.829$, $p = .001$ (Figure 3a) and these responses were also slower, $F(1,33) = 14.575$, $p = .001$ (Figure 3b). Rats maintained in enriched conditions were slower to avoid shock than those in standard cages, $F(1,33) = 6.722$, $p = .015$ (Figure 3b).

DISCUSSION

Our experiment has shown that rats maintained in an enriched environment need less stimulation (lower NS coefficient) than rats maintained in a standard environment. This finding supports the data of Matysiak and Toeplitz (1990). Earlier research (Sackett, 1967; Hennessy et al., 1976; Tees et al., 1980) revealed an opposite effect. This may be due to the fact that earlier researchers did not sufficiently distinguish

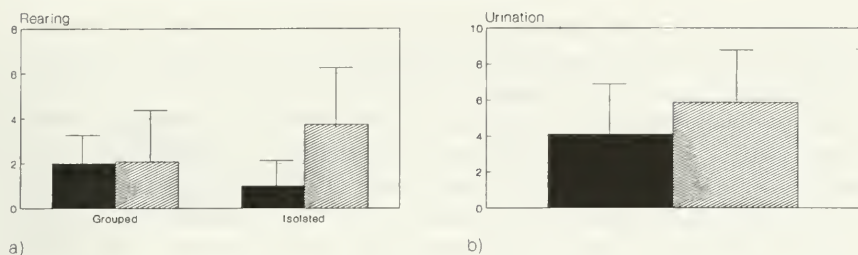


FIGURE 2. Means and standard deviations of: a) rearing, ■ standard, ▨ enriched; b) urinations in the open field, ■ grouped, ▨ isolated.

between exploratory behavior and general motor activity; the same indicators may show different kinds of activity. For example, bar pressing may be an indicator of exploration during the first 30 min of the test but cannot play such a role in an unchanged situation after 20 hours on the one hand. Behavior aimed at supplying the organism with sensory stimulation may play a role on the other hand. Our finding for the initial, 90-min period of testing rat activity in the activity wheels and in the open field (rearing) corroborate earlier findings. We believe that exploration is the most important kind of activity during this phase of wheel running. Rats maintained in the enriched environment ran more than control rats in the "light" wheel and seemed to explore more intensively in the open field, although this was not an interaction effect of physical and social enrichment. These results are in general accordance with Manosevitz (1970), Renner and Rosenzweig (1986) and Renner (1987).

We believe our results confirm the view that different mechanisms are responsible for exploratory behavior and behavior contingent on the need for sensory stimulation. The term used to explain the individual level of need for stimulation is the coefficient of transformation of stimulus strength suggested by Matysiak (1985). This hypothetical (physiological) mechanism causes individual differences in stimulation processing. The same stimuli may be stronger or not for different individuals. Drops in need for sensory stimulation can be interpreted as manifestations of

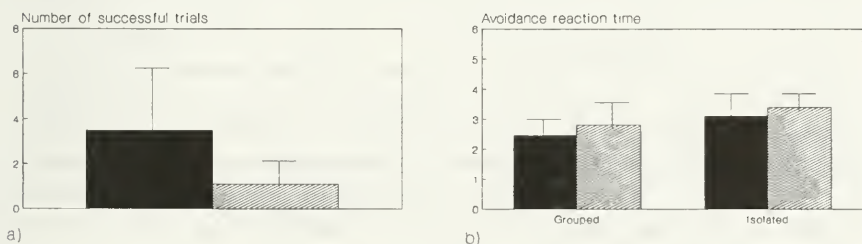


FIGURE 3. Means and standard deviations of: a) number of correctly performed avoidance responses during two sessions (twenty trials), ■ grouped, ▨ isolated; b) avoidance reaction time, ■ standard, ▨ enriched.

increases in individual reactivity. This reactivity is defined in terms of the value of the coefficient of transformation of the stimulus strength.

We finally found an increase in emotional reactivity (urination and defensive responses) in our socially isolated rats and a decrease of emotional reactivity in rats maintained in enriched conditions. This is in accordance with the theory of Denenberg (1964) and later findings of Baenninger (1967), Koch and Arnold (1972), Parker and Morinan (1986), and gives added support to the view that the social environment is decisive for the development of the emotional sphere.

EXPERIMENT TWO

Experiment Two was similar to Experiment One, the difference being that 60–70 day-old rats were studied in the experimental treatments.

Animals

Forty-eight outbred male Wistar rats were tested.

Procedure

All experimental manipulations were as in Experiment One. The rats were 60–70 days old when the experiment started. Until the experimental treatment started, the rats were maintained in standard (see Experiment One) cages in groups of six.

RESULTS

Behavior during 90 Min of Measurement in Self-exposure Chamber and Activity Wheels. Analysis of activity in the self-exposure chamber revealed that animals maintained in standard conditions were much more active than rats maintained in the enriched environment, $F(1,37) = 13.765$, $p = .001$ (Figure 4a).

Significantly greater activity was found in the activity wheels in animals maintained in groups as compared with socially isolated animals. This was found both in the light wheel, $F(1,40) = 8.904$, $p = .005$ (Figure 4b), and in the control wheel, $F(1,40) = 9.313$, $p = .004$ (Figure 4c).

Rat Behavior during 22 H Test Period in Self-exposure Chamber and Activity Wheels. Analysis of the variance of the need for light stimulation (NS-coefficient computed according to complete formula) revealed a significant interaction of the experimental variables, $F(1,34) = 5.901$, $p = .021$ (Figure 5a). Isolated rats, maintained in standard conditions, revealed a larger need for light stimulation than isolated rats maintained in an enriched environment.

As concerns activity in the activity wheels, rats maintained in groups were significantly more active than rats maintained in social isolation.

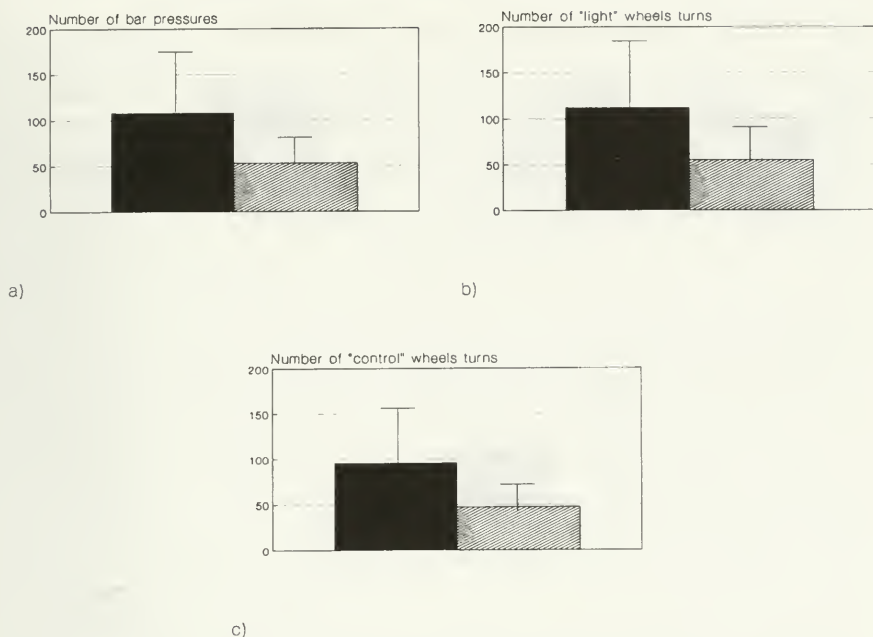


FIGURE 4. Means and standard deviations of: a) number of pressures on both bars during first 90 min of measurement in self-exposure chamber, ■ standard, ▨ enriched; b) number of light wheels turns during first 90 min of measurement, ■ grouped, ▨ isolated; c) number of control wheels turns during first 90 min of measurement, ■ grouped, ▨ isolated.

This relationship holds both for the light wheel, $F(1,40) = 18.806$, $p = .001$ (Figure 5b) and the control wheel, $F(1,40) = 12.192$, $p = .001$ (Figure 5c).

Behavior in the Open Field. Analysis of behavior in the open field showed that rats maintained in the standard environment reared more than rats maintained in the enriched environment, $F(1,43) = 4.551$, $p = .039$ (Figure 6).

Acquisition of Defensive Response. No differences were found in defensive responses.

DISCUSSION

An important finding from Experiment Two is the different relationship between environmental factors and need for light stimulation than in Experiment One. We may thus conclude that the strength and direction of changes in behavior due to environmental experience are contingent to a significant extent upon the developmental phase in which the environmental experience took place.

There is an important limitation of such a conclusion. The animals

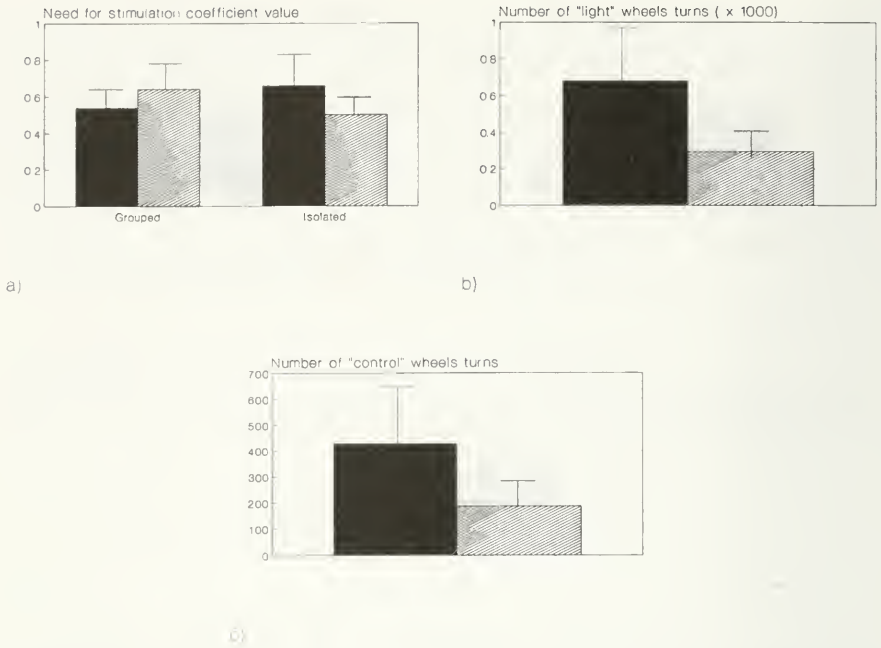


FIGURE 5. Means and standard deviations of: a) need for stimulation coefficient $NS = [Ne/(Ne + Nc)] \cdot [Te/(Te + Tc)]$ computed on the base of second, 22 h phase of measurement in the self-exposure chamber, ■ standard, ▨ enriched; b) number of wheels turns during second, 22 h phase of measurement, ■ grouped, ▨ isolated; c) number of control wheels turns during second, 22 h phase of measurement, ■ grouped, ▨ isolated.

spent different amounts of time in the experimental conditions in Experiment One and Experiment Two. Thus, the differences in results of those two experiments may be due, to some extent, to experience before observation, such as the duration of housing. We believe such an interpretation would probably be true if the obtained differences were only quantitative. However, as we obtained different directions of change in the dependent variables in these experiments, we infer that these differences were related to the different developmental phase of the animals

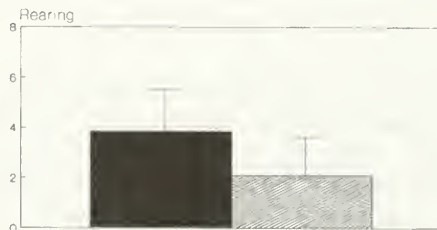


FIGURE 6. Means and standard deviations of rearings in the open field, ■ standard, ▨ enriched.

when given the experimental treatment in Experiment One and in Experiment Two.

Attention must also be drawn to the finding that social environment affects need for kinesthetic and tactile stimulation (22 h test in activity wheels). Rats are "contact" animals (Marler & Hamilton, 1966), i.e., they seek physical contact with their partners. The tactile sense is crucial in this context. Hence when tactile stimulation is restricted, this could have a marked effect on those behaviors which reflect need for tactile and kinesthetic stimulation.

Different kinds of exploratory behaviors were affected by both social and physical environments as shown in the results from the first 90 min in activity wheels, self-exposure chamber and open-field. It is noteworthy that enriching the environment in Experiment Two, as opposed to Experiment One, led rather to a decrease in intensity of exploration. A significant role of the social environment also emerged in regulation of such behavior. Rats maintained in groups were more exploratory than rats maintained in social isolation. This finding corroborates that of Parker and Morinan (1986). The lack of interaction of experimental factors is also noteworthy.

As compared with Experiment One, changes in emotional reactivity due to social isolation were weaker. This is in accordance with the conclusion of Denenberg (1964) and Einon and Morgan (1976) who wrote that the critical period for social isolation in rats is the early phase of development.

GENERAL DISCUSSION

The general purpose of the conducted studies was the examination of the effects of environmental influences on temperamental traits in rats. According to the traditional point of view (Strelau, 1983), temperamental traits are strongly determined by genetic factors, the environmental effects recognized as rather secondary or additional. This way of thinking was especially strong with respect to so called "lower mammals." Our studies have shown a significant role of environmental experience in the development of temperament in rats. We draw attention to the fact that different environmental effects were found depending on the age of rats at which experimental treatment started.

Strelau (1983) claims that the social environment affects temperament via formal features, i.e., excessive or insufficient stimulation. Our studies have shown that specific types of stimulation differentially affect specific temperamental features. In general, we agree with Strelau, but we must underscore that various modalities of stimulation specifically affect different features of temperament. This specificity changes as animals grow older. Thus, the qualitative aspect of sensory stimulation is also important for temperament development. The role of qualitative properties of

sensory stimulation have been pointed out, so far, for the development of intelligence and abilities.

Our findings do not permit any unequivocal conclusions as to the categories of environmental factors which affect temperament. We may put forward the opinion, however, that emotional reactivity in rats and their need for tactile stimulation are more affected by social experience of the individual rats whereas need for light stimulation is more affected by the physical environment. It draws our attention to the possible, common evolution of the sensory systems and temperamental traits.

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INCREASED TURN ALTERNATION BY WOODLICE (*Porcellio scaber*) IN RESPONSE TO A PREDATORY SPIDER, *Dysdera crocata*

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ABSTRACT: The common garden woodlouse (*Porcellio scaber*) is known to alternate turns (correcting behaviour), but the function of this behaviour is only poorly understood. We investigated Hughes' (1967) hypothesis that this behaviour enables woodlice to escape efficiently from unfavourable environmental conditions by considering the effect of contact with a predator, a potentially unfavourable environmental condition that has not been investigated previously. In experiments, woodlice alternated turns more frequently after contact with a known predator of woodlice (*Dysdera crocata*) than after contact with cotton wool or a nonpredatory arthropod (housefly, *Musca domestica*).

Many animals (Hughes, 1989) are known to alternate turns when they encounter obstacles: i.e., successive turns tend to be in opposite directions ("correcting behaviour"). Correcting behaviour has been shown in vertebrates and invertebrates, the latter including centipedes (Schäfer, 1972), earwigs (Schäfer, 1982) and woodlice (Hughes, 1967). Although the function of this behaviour is not well understood, Hughes (1967) suggested that one function of alternating turns by *Porcellio scaber*, the common garden woodlouse, might be to ensure efficient, direct movement away from biologically unfavourable conditions. Thus, by alternating turns upon encountering obstacles, an individual animal can move more efficiently away from a given area than would be possible as a result of a series of random turns. In support of this hypothesis, Hughes (1967, 1978) showed that *P. scaber* alternated turns more consistently when deprived of food or desiccated, than when well fed or kept in moist conditions.

Data are needed to ascertain whether other unfavourable conditions,

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in addition to food and water shortage, influence the rate at which woodlice alternate turns. In the present paper, we show that contact with *Dysdera crocata*, a spider which preys on woodlice, influences *P. scaber*'s correcting behaviour.

MATERIALS AND METHODS

Animals

Porcellio scaber is a well-known cosmopolitan terrestrial isopod. Being a crustacean, it is restricted to damp environments such as beneath stones or rotting vegetation. The vertebrate predators of *P. scaber* include birds, mice, shrews, hedgehogs, lizards, toads, frogs, and newts (Gorvett, 1956). However, *P. scaber*'s most significant predators are probably spiders (Bristowe, 1947). *Dysdera crocata*, the spider we used in the present study, is known to be a particularly important predator of *P. scaber* in nature (Bristowe, 1941; Cooke, 1965; Sunderland & Sutton, 1980). For controls, we used common houseflies, *Musca domestica*, and balls of cotton wool.

P. scaber and *D. crocata* were both collected from suburban Christchurch gardens, then cultured in the laboratory using standard methodology (Jackson & Pollard, 1982). Houseflies also were cultured in the laboratory. The size of animals in tests was standardized: adult *Dysdera crocata* (body length: c. 12 mm), adult *Musca domestica* (c. 8 mm), and large adult and juvenile *Porcellio scaber* (c. 10 mm).

Apparatus

Hughes (1967) tested woodlice in transparent Perspex mazes. Our test apparatus (Figs. 1–3) was a modification of Hughes' maze, the primary difference being that we provided a starting chamber (diameter 25 mm, height 55 mm) in which the stimulus animal (spider or fly) could be restrained and into which the woodlouse was placed.

The maze was set on a white paper base on a table and illuminated evenly by two fluorescent ceiling lights (65 watts) 1.6 m overhead. There was an opening in the starting chamber (Fig. 1) through which the woodlice could exit into an alley (40 mm × 8 mm × 8 mm) leading to a forced right turn (Fig. 2). From here, a woodlouse could then travel down a ramp and confront an initial T junction (point C, Fig. 2). The design of the maze required the woodlouse next to make another three "decision turns" before reaching an end point (Fig. 3). The woodlouse's eventual end point could therefore be the result of either three, two, one or no alternating turns following the initial forced turn at point C (Fig. 3). Therefore, each woodlouse's end point could be expressed as one of four fractions (i.e., 0/3, 1/3, 2/3, 3/3) indicating rate of alternation following

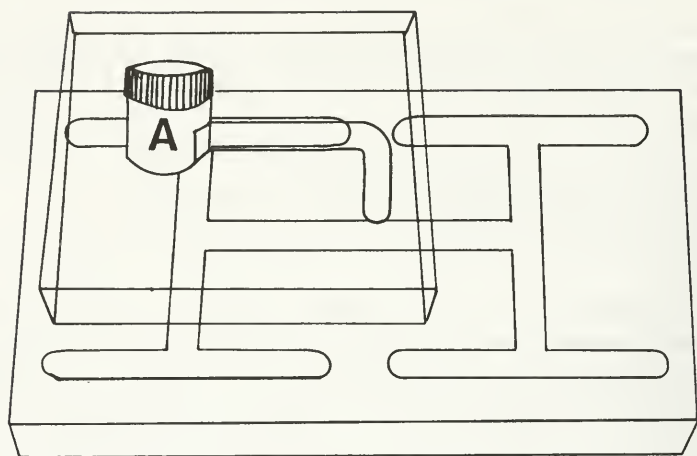


FIGURE 1. Drawing of test apparatus. Woodlouse placed in starting chamber (A) before allowed to enter maze (below).

contact with the stimulus animal in the starting chamber. Data were analysed using the Kruskal-Wallis one-way ANOVA, with Bonferroni adjustments for subsequent simultaneous comparisons (Rice, 1989).

Procedure

In an experimental test, a woodlouse was put in the starting chamber with a *Dysdera crocata* ("spider"). In a control test, a woodlouse was

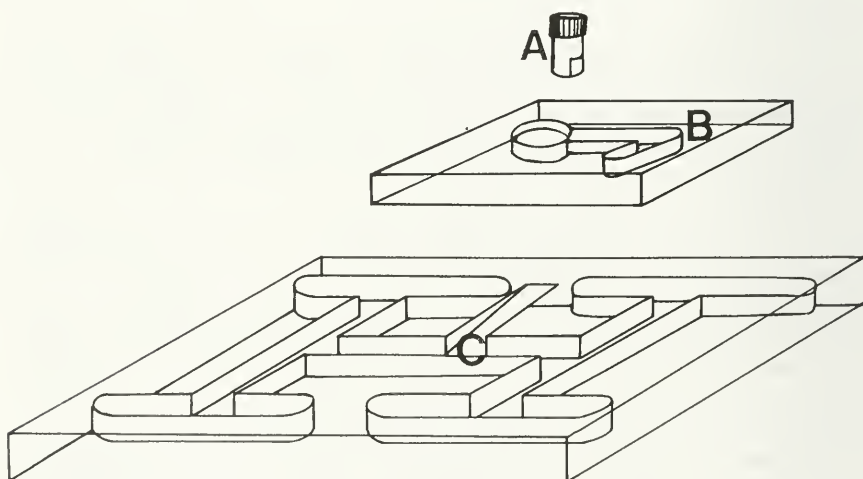


FIGURE 2. Exploded diagram of test apparatus. Woodlouse moves from starting chamber (A) to 8×8 mm alley which leads to forced right turn (B) and down ramp to initial T junction (C). From here woodlouse is free to walk through maze to an end point.

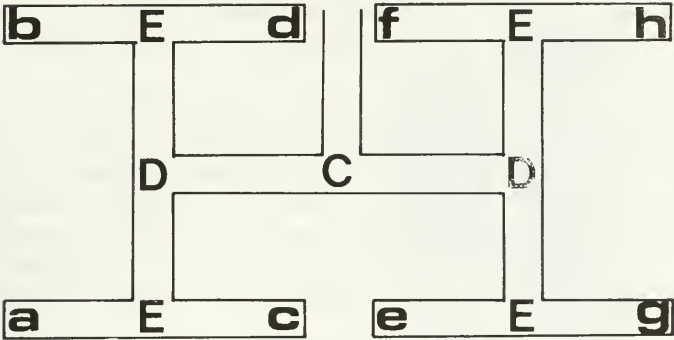


FIGURE 3. Floor plan of maze. At bottom of ramp, woodlouse is confronted by initial T junction (C) where it also has choice of turns at points labelled D and E. From E, woodlouse can proceed to one of eight possible end points (a, b, c, d, e, f, g, or h). Finishing point of woodlouse recorded as $a = 2/3$, $b = 1/3$, $c = 1/3$, $d = 0$, $e = 1/3$, $f = 1/3$, $g = 3/3$, or $h = 2/3$.

put in the starting chamber with either a ball of cotton wool or a *Musca domestica* (“fly”).

The ball of cotton wool was c. 10 mm in diameter. Tests using balls of cotton wool were controls for the effect on woodlice of encounters simply with objects comparable in size to *D. crocata*. Flies are nonpredatory arthropods similar in size to *D. crocata*. Wings were removed from flies so that, like the spiders, the flies could move about in the starting chamber by walking but not by flying. Tests using flies were controls for the effect on woodlice of encounters simply with animals comparable in size to *D. crocata*. By comparing data from tests using *D. crocata* to data

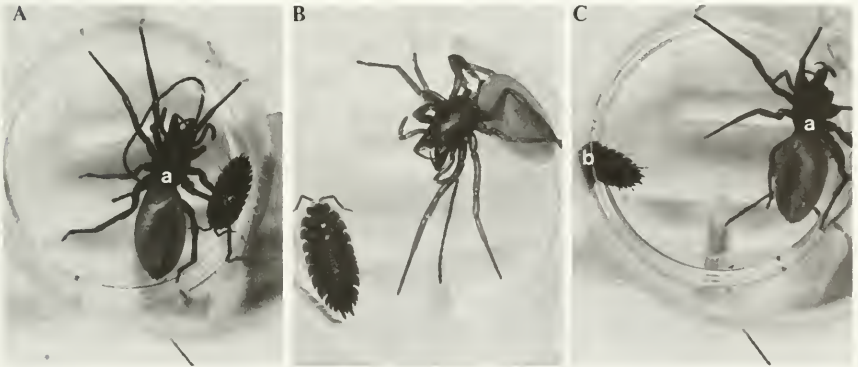


FIGURE 4. View into starting chamber where stimulus (in this instance, spider) contacts woodlouse. A: stimulus secured by cotton thread (a) with sufficient slack to allow interaction with woodlouse. Exit closed (b). B: thread (a) tightened, pulling spider up against side of starting chamber, thereby ending interaction before woodlouse can be attacked. C: starting chamber rotated to open exit hole (b) and allow woodlouse to enter maze.

from controls, we could ascertain whether increased rates of alternating turns was a response by woodlice specifically to the encounters with the predator.

The spider or fly was first immobilised with carbon dioxide. Next, a cotton thread (Fig. 4A) was tied around the spider (between its cephalothorax and abdomen) or fly (between its thorax and abdomen). The other end of the thread was then held by hand at a length which allowed the stimulus animal sufficient slack to move throughout the starting chamber but insufficient to permit escape from it. Each spider and fly was used repeatedly in multiple tests. However, each woodlouse was tested only once.

The woodlouse to be tested was carefully pushed into a glass vial with an artist's brush, then gently dropped into the starting chamber. The lid was then placed on the chamber to start a test.

In a successful test, the woodlouse was contacted by the spider (Fig. 4A), fly, or cotton wool. As soon as this happened, we tightened the thread to draw the spider, fly, or cotton wool tight against the side of the chamber opposite the exit hole (Fig. 4B). Next, the exit hole was opened to provide the woodlouse access to the maze (Fig. 4C). Once in the maze, the woodlouse could run freely and its end point was recorded (Fig. 3).

If a woodlouse failed to reach an end point within 2 min after contacting the spider, fly, or cotton wool, or if at any time the woodlouse backtracked, the test was aborted. Fortunately such events occurred in fewer than 10% of the trials. Between trials, the maze was wiped off, first with ether, then with distilled water, after which it was wiped dry with clean cotton wool. Following each trial, the paper base under the maze was replaced.

For each of the three treatments, there were 100 trials. The starting chamber was occupied by: treatment 1) a tethered spider (to test for the effect of the predator); treatment 2) a tethered ball of cotton wool (a control for the effect of spider-size objects); or treatment 3) a tethered fly (a control for the effect of spider-size nonpredatory arthropods).

RESULTS AND DISCUSSION

Using the Kruskal-Wallis one-way ANOVA, the effect of treatments (Fig. 5) was found to be highly significant ($p < .001$), thus justifying subsequent use of post hoc comparisons between individual treatments. Woodlice made significantly more alternating turns after contact with a predatory spider than after contact with a fly ($p < .01$) or a ball of cotton wool ($p < .005$), but there was no significant difference in the alternation rates when contact with a fly was compared to contact with a ball of cotton wool. Therefore, the effects on woodlouse correcting behaviour that we observed in tests using *D. crocata* appear to be caused by specific

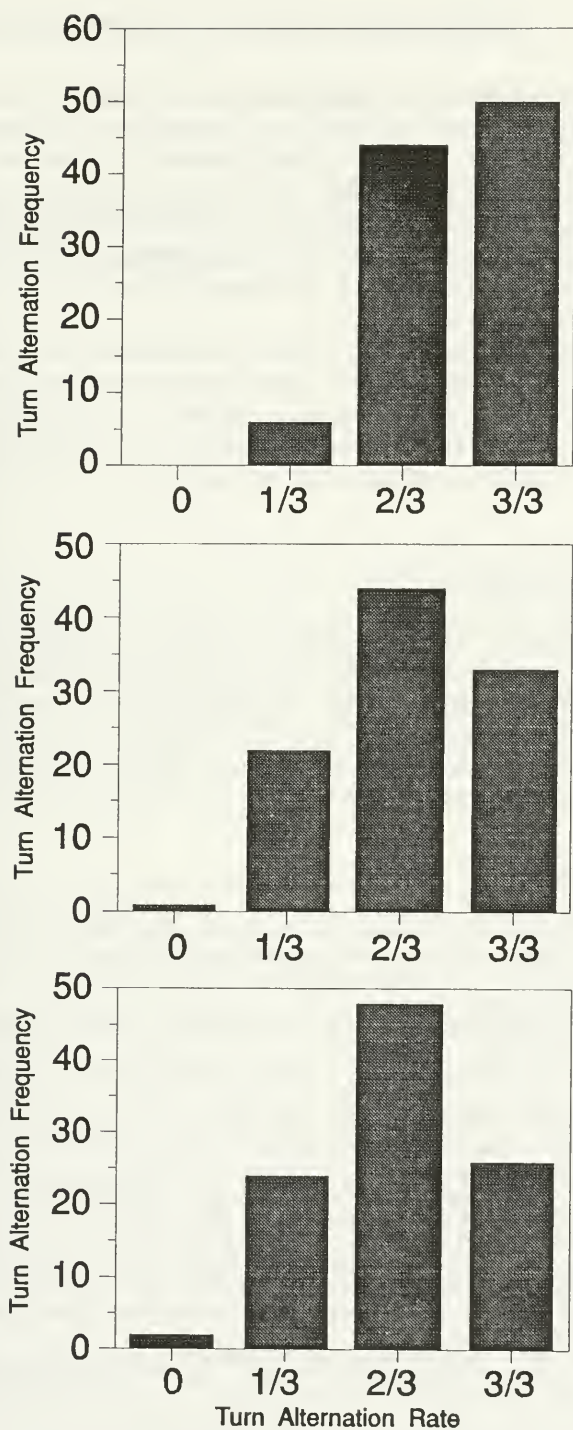


FIGURE 5. Results from testing *Porcellio scaber* with, from top, *Dysdera crocata* (A), *Musca domestica* (B), and cotton wool (C).

cues from this predator, not by generalised stimuli from inanimate objects or from animals of a size comparable to the predator. We do not know exactly what cues from *D. crocata* are important, but they are evidently something other than the predatory behaviour of the spider because we always pulled the spider back before it could attack the woodlice. We suggest that chemical cues from *D. crocata* are important because woodlice species are known to have well-developed abilities to discern chemical stimuli (Sutton, 1972).

Hughes (1967) proposed that correcting behaviour may function to facilitate efficient movement away from unfavourable conditions. The results of this study support Hughes' hypothesis by providing evidence that woodlice react to the presence of a predator (an unfavourable condition not previously investigated) by increasing their rates of alternating turns.

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COURTSHIP BEHAVIOR IN THE MALE GUPPY (*Poecilia reticulata*): A GENETIC ANALYSIS

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ABSTRACT: Courtship behavior in the male guppy (*Poecilia reticulata*) was analyzed employing 13 behavioral sequences measured in standardized situations. The stability of these measurements allowed a systematic study of individual differences and of their origins. Factorial analyses lead to two distinguishable main categories of behaviors: one was related to gonopodial swinging; the other to sigmoid display. Variables used to describe gonopodial swinging have only environmental correlates. The additive genetic component was null when estimated by two independent genetic analyses and this result was confirmed by a nonresponse to directional selection. On the contrary, most of the variables used to describe sigmoid display exhibit significant additive genetic components and this was confirmed by the incidence of males exhibiting vs. not exhibiting this behavior in a replicated directional selection. The adaptive significance of the variables is discussed in the light of genetic and observed correlations between the phenotypes.

RÉSUMÉ: Le comportement de cour du male guppy a été analysé à partir de 13 séquences comportementales relevées dans une situation standardisée. La stabilité des mesures autorise une étude systématique des différences individuelles et de leurs origines. Des analyses factorielles conduisent à dégager deux catégories de comportements: l'une est relative aux mouvements du gonopode, l'autre au développement de sigmoïdes. 1) Les variables décrivant les mouvements du gonopode semblent n'être affectées que par les facteurs d'environnement. Deux analyses indépendantes, conduisant à l'estimation des composantes génétiques additives, fournissent des valeurs nulles. Ce résultat est confirmé par l'absence de réponse à la sélection pour la variable nombre de mouvements du gonopode, au cours d'une expérience de sélection directionnelle. 2) Au contraire, la plupart des variables mesurant les caractéristiques des sigmoïdes sont affectées par une part de variance génétique additive, significativement différente de zéro. Conformément à l'hypothèse attendue dans le cas où la variance génétique additive est significative, le trait *présence* opposé à *absence* de sigmoïde durant le test, répond à la sélection. La valeur adaptative de ces traits est discutée à la lumière des corrélations phénotypiques et génotypiques.

Twenty years ago, Barlow (1981) lamented the lack of knowledge concerning the genetic correlates of "modal action patterns" that he defined

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as "a subset of patterned motor outputs" or the "chunks of behavior animals perform that have a statistically recognizable pattern such as displays, specialized feeding behavior and some actions involved in bodily care." Since then, the situation has hardly changed, if we except species such as *Drosophila* (Sokolowski, 1992; Ringo, Dowse, & Barton, 1986; Ringo, Dowse, & Lagasse, 1987; Ricker & Hirsch, 1988). However, species such as fishes in which the modal action patterns are particularly well documented, provide an ethological framework for the study of individual differences and their genetic or environmental correlates. Data are generally limited to crosses between hybridizing species: territoriality in *Macropodus opercularis* and *M. opercularis concolor* (Vadasz, Kiss, & Csanyi, 1978), social dominance in *Salvelinus namaycush* and *S. fontinalis* (Ferguson & Noakes, 1982), and courtship behavior between *Xiphophorus helleri* and *X. maculatus* (Clark, Aronson, & Gordon, 1948, 1954) or between *Lepomis gibbosus* and *L. macrochirus* (Ballantyne & Colgan, 1978). Indeed interspecific hybrids provide an analytical perspective otherwise unavailable and, moreover, are informative about phylogenetic relationships (Hirsch & McGuire, 1982). These crosses, thus, provide useful information that is complementary to intraspecies genetic analysis, particularly with long term selection that enlightens the evolutionary factors.

There have been very few attempts at intraspecies behavior-genetic analysis in fishes, in spite of several elegant studies: locomotor behavior (Gerlai, Crusio, & Csanyi, 1990), social behavior (Francis, 1984) in *Macropodus opercularis*, aggression in *Gasterosteus aculeatus* (Bakker, 1985, 1986), and social composition or interaction between males in *Poecilia reticulata* (Farr, 1983). The small fish called the fanciers' Guppy, or *Lebistes reticulatus* (now *Poecilia reticulata*) is a good model for genetic analysis. It has a long history both in genetics and behavior studies. A Y-linked inheritance has been demonstrated for a color marker (Schmidt, 1920). Other Y, X and autosomal genes correlated with colored and morphological variants were discovered by Winge (1923), Winge and Didlesen (1947) and the list has been lengthened since these pioneering works (see Yamamoto, 1975 for a review and Phang, Ng, & Fernando, 1989 for complex inheritance of color patterns). On the other hand, the behavior of *P. reticulata* has been extensively described by ethologists, particularly for courtship behavior in males (Haskins & Haskins, 1950; Baerends, Brouwer, & Waterbolk, 1955). Liley (1966) described for *P. reticulata* several courtship displays that are not present in the sympatric species *P. vivipara*, *P. parae* and *P. picta*.

The purpose of the present paper is to analyze the structure of individual differences in the male courtship behavior of *P. reticulata* and their genetic correlates: genetic components of the variation and response to selection.

EXPERIMENT 1: INDIVIDUAL DIFFERENCES IN MALE COURTSHIP BEHAVIOR

The previously published ethologic descriptions provide many variables describing specific courtship behavior in *P. reticulata* males. The prerequisite of the genetic analysis is the detection of the variables that are susceptible to disclose stable differences between males in a standardized test.

Animals. The males came from a heterogeneous population developed for the experiments presented here. Eight populations were at its origin: seven stocks having been selected for independent history were provided by fanciers and one population was directly imported from Guyana. The eight populations were crossed two by two, giving four F_1 s; their crosses gave two F_2 s; these were used to produce an F_3 heterogeneous population that included 422 males used in the different experiments.

Breeding Conditions. As a general rule, the females were isolated from males in an individual tank after fecundation and removed as soon as parturition was observed. Each tank ($39 \times 21 \times 19$ cm) was individually supplied with filters under sand, aeration and plants: *Elodea canadensis* and *Lemna polyrrhisa*. *Fontinalis antipyretica* was added when necessary to provide a protective device for the fry against female cannibalism. Pregnant females were fed with living *Artemia*, experimental subjects with standardized commercial dry food and fry with hard-boiled egg yolk. Temperature was kept at $24.9 \pm .9^\circ\text{C}$, pH 7.5 to 7.8, photoperiod 11/13 hours with light on at 7 pm.

Behavioral Observations. These were performed during the light period with 180 ± 7 day old males maintained by separated pairs of brothers from the age of 30 days until the test (except in Experiment II) to avoid possible effects due to isolation. A glass tank having three compartments was used for the observations. The two lateral compartments, each divided into four opaque boxes, were assigned to males selected for the observations. The central part ($40 \times 30 \times 18$ cm) was used for behavioral testing. Each of the eight boxes was connected to the central part by holes (30 mm in diameter) located 40 mm under the surface of the water, and closed by a trap. The physical conditions were identical to the rearing tanks except that there were neither plants nor food.

The female was placed in the central part. Only females 4–29 days after parturition were chosen since the physiological state of the female has been shown to affect courtship frequency of the male in this species (Liley, 1966). One hour later the entrance gate of the first hole was gently lifted so that the male could enter. The behavioral recordings lasted 20 min starting when one of the behavioral sequences described below appeared.

Prior to the beginning of courtship, the male follows the swimming female positioned 2 to 3 cm behind the female. This first variable labelled

"time spent following the female" is abbreviated: I. *Time following*. The male then assumes a position in front of the female before beginning the display, and then makes a more or less complete circle around the female. The "number of circles around the female" is abbreviated: II. *Nb. circles*. Another pattern of behavior has been described (Baerends et al., 1955) for this stage of courtship. The general axis of the male's body is directed toward the body of the female. The male is watching the female, the dorsal and caudal fins being folded and slight quiverings of the male's body may be observed (labelled "number of watching positions": III. *Watching*).

Two other behavioral sequences are of the greatest importance for the present paper: gonopodial swinging and sigmoid display, interrupted by orientation patterns.

Gonopodial swinging forward is performed independently of copulation or copulation attempts. Generally the movement is performed when the male is motionless, and the snout directed toward the snout of the female. The movement was either performed alone by the male: (IV. *Nb. simple gonopodial swingings*) or associated with incurvation of the body and with spreading the fins: V. *Nb. complex gonopodial swingings*. The reciprocal of the first gonopodial swinging latency, either simple or complex (VI. *1/first gonopodial latency*) and a composite score summing variables IV. and V. (XIII. *Nb. gonopodial swingings*) will be used in further steps of genetic analysis.

The sigmoid display was first described by Clark, Aronson & Gordon (1948, 1954): the body is arched, both tail and head away from the female. This posture is held for 5 to 50 sec in some individuals. The body, the pectoral, and caudal fins quiver rapidly. Generally, the male remains in the same place but may on occasion move backward and forward. During the sigmoids, the fins may be more or less spread. The frontal sigmoid begins when the male is in front of the female, the male body perpendicular to the axis of the female's body. The lateral sigmoid starts when the male is parallel to the female, the head being in the same or in the opposite direction. These two behaviors were pooled (VII. *Nb. sigmoids*) since there are many intermediate patterns and a lateral sigmoid may become frontal and vice-versa during the display. The total durations of these sigmoids during the observation (VIII. *Duration sigmoids*) and the reciprocal of the latency of the first sigmoid, either lateral or frontal (IX. *1/latency first sigmoid*) were noted. Furthermore, we calculated the average duration of all the sigmoids, either lateral or frontal (X. *Average duration sigmoids*) except the weak. The variable XI. *Nb. weak sigmoids* refers to sigmoids with a low intensity form, the body being in "an arched and not very pronounced sigmoid shape" (Liley, 1966). Thrusting, copulation and copulation attempts are characterized by gonopodial contact or attempted contact (XII. *Nb. copulations*). Whether insemination is accomplished or not has not been considered and consequently the post-

TABLE 1
Reliability of Variables Used to Measure Courtship Behavior

<i>Variables</i>		<i>Split half</i>	<i>Test retest</i>
I	Time following	.17	.16
II	Nb. circles	.01	.05
III	Watching	.59	.45
IV	Nb. simple gonopodial swingings	.62	.63
V	Nb. complex gonopodial swingings	.91	.77
VI	1/first gonopodial latency	ND	.89
VII	Nb. sigmoïds	.84	.97
VIII	Duration sigmoïds	.67	.78
IX	1/latency first sigmoïd	ND	.85
X	Average duration sigmoïds	.77	.81
XI	Nb. weak sigmoïds	.62	.71
XII	Nb. copulations	ND	.63
XIII	Nb. gonopodial swingings (IV + V)	.86	.93

ND: not done.

ejaculation jerk (Clark, Aronson & Gordon, 1948, 1954) has not been taken into account here.

Statistics. Split half (between the two parts of the first test, except for latencies), and test/retest (25 ± 5 days later) were computed to test for the reliability of the measurements. Fifty males were tested twice. A factor analysis (principal components method) was performed on their scores at the first test after exclusion of the least reliable variables. In all cases scale transformations were carried out to ensure normality of the distribution scores to allow the use of product moment correlations and R^2 as diagonal values. In order to confirm the factorial structure of the variables selected for the genetic analysis, a new sample of 115 males was observed. The following variables were included in the factor analysis: the composite variable XIII. *Nb. gonopodial swingings* (sum of variables IV. and V.), VI. (*1/first gonopodial latency* either simple or complex gonopodial swinging), VII. (*Nb. sigmoïds*), VIII. (*Duration sigmoïds*), and IX. (*1/latency first sigmoïd*), X. *Average duration of sigmoïds* (excluding the weak sigmoïds).

Results and Discussion. Most of the reliability coefficients exhibit values that are high enough to ensure behavioral or genetic analysis (Table 1).

The first factor analysis (Table 2) performed with all the variables (excluding variables I and II, having insufficient reliability) led to the extraction of two factors. After rotations (maximization of loadings as

TABLE 2
Loadings in the First Factor Analysis of Variables Used to Measure Courtship Behavior

	<i>Variables</i>	F_1^*	F_2	F_1'	F_2'	<i>Com-mon-alities</i>
III	Watching	.42	-.06	.37	-.20	.18
IV	Nb. simple gonopodial swingings	.64	.62	.84	.29	.79
V	Nb. complex gonopodial swingings	.58	.55	.73	.33	.64
VI	1/first gonopodial latency	.19	.32	.30	.22	.14
VII	Nb. sigmoïds	.72	-.33	.54	-.59	.63
VIII	Duration sigmoïds	.88	-.25	.70	-.60	.85
IX	1/latency first sigmoïd	.56	-.34	.38	-.54	.44
XI	Nb. weak sigmoïds	.70	-.22	.73	.40	.27
XII	Nb. copulations	.13	.50	.33	.40	.27

* F_1 F_2 before and F_1' F_2' after rotations.

criteria) the first factor can be interpreted as a general factor taking 38% of the variance into account, with all the loadings being higher than .30. The second factor (18% of the variance) was defined by the opposition between variables describing sigmoïd display on the one hand (VII. *Nb. sigmoïds*, VIII. *Duration sigmoïds*) and gonopodial swinging on the other (IV. *Nb. simple gonopodial swingings*, V. *Nb. complex gonopodial swingings*, VI. *1/first gonopodial latency*), and XII. *Nb. copulations*. In the second analysis, the first factor (49% of the variance) has only positive loadings, whereas the second (33%) only presents loadings higher than .30 for gonopodial swinging measurements (Table 3).

Some differences appear in the percentages of variance explained by

TABLE 3
Loadings in the Second Factor Analysis of Measures of Courtship Behavior (Rotated Factors)

	<i>Variables</i>	F'_1	F'_2
XIII	Nb. gonopodial swingings	.54	.39
VI	1/first gonopodial latency	.27	.44
VII	Nb. sigmoïds	.82	-.20
VIII	Duration sigmoïds	.91	-.08
IX	1/latency first sigmoïd	.69	-.14

each of the factors in the two analyses. This was expected due to differences in the selected variables. However, the two factorial structures can be interpreted in the same way: first, they show a common part of variance for the variables used to describe the behavioral sequences observed during courtship and, moreover, suggest a distinction between variables measuring gonopodial movements on the one hand and sigmoid display on the other. The variables used for the second analysis, covering these two categories of behaviors, were hence considered for environmental and genetic analyses.

EXPERIMENT II: EARLY ENVIRONMENTAL VARIATION AND ADULT COURTSHIP BEHAVIOR

Do environmental variations such as the size of the brood and the density of population during the early postnatal period affect courtship in adult males?

Environmental Modifications. Males were taken from the heterogeneous stock and two rearing conditions were considered: first the size of the brood: 30 males from the small (less than 20 offspring) and 30 from large broods (greater than 20 offspring) were compared; second the length of exposition to high population density: two groups of 15 subjects each were constituted by taking individuals from pairs separated from the brood at 25 days or another separated at 45 days of age. The six behavioral variables defined at the end of the first experiment were measured in the previously defined conditions and compared by a *t* test.

Results and Discussion. The size of the brood only affects VII. *Nb. sigmoïds*: Males from small broods had a higher performance than those from large broods (20.26 ± 1.97 vs. 17.03 ± 2.13 , $p < .05$). As concerns age at separation from the brood, subjects separated earlier showed significantly more courtship behavior than the others: 25.94 ± 3.20 vs. 12.11 ± 4.34 for VII. *Nb. sigmoïds* ($p < .01$), 199.31 ± 7.56 vs. 80 ± 4.23 for XIII. *Nb. gonopodial swingings* ($p < .01$). The other variables present tendencies in the same direction without reaching the $p < .05$ significance level.

EXPERIMENT III: GENETIC COMPONENTS OF THE VARIATION

The genetic method was imposed by the features of the species: no inbred strains (in the narrow sense) at the beginning of the experiment and difficulty in performing individual diallic crosses since the females keep spermatozoa alive for several months.

Genetic Design. Two genetic designs were performed to estimate the main components of variation: an offspring-one parent (O-O.P) and a half-sib (H-S) design. These two methods can provide an accurate es-

timation of the additive component (Jinks & Broadhurst, 1965; Dawson, 1965; Kearsy, 1965; Mather & Jinks, 1971), that could be of particular interest in the present study since some of them will be used to predict the success of directional selections. Moreover, full-sib correlations were calculated.

For the O-O.P design, 34 males were mated with 34 virgin females; for each variable, the male value and the averaged score of its male progeny were analyzed according to the methods described by Falconer (1960, 1963). For the H-S design, 118 males were individually mated each with 3 virgin females. In the two experiments every subject was taken from the heterogeneous population: males came from different families and were also mated with non-sister females. The males came from pairs separated from broods including between 15 and 25 individuals at 30 ± 3 days.

The scores of the offspring in the H-S design were analyzed according to Falconer (1960, 1963) and Mather and Jinks (1971) with an ANOVA method for nested designs with unequal size (Snedecor & Cochran, 1967) because not all the females were fecundated and the numbers of males differ across their progenies. The genetic correlations among the 6 previously described behaviors were calculated by the cross-covariance method (Falconer, 1960). Appropriate transformations were made to fulfil the technical requirements of ANOVA for individual scores ($\log_{10}(C + x)$), C being different for each variable.

Test for Independence of Genotypic and Environmental Effects. The different models assume that the interaction between the genotype of the population and environment to which they are exposed in this population has no effect upon the observed variance. When a population is in Hardy-Weinberg equilibrium, the gene frequencies can be assumed to be identical from one generation to the next, particularly in the father and son generation of our populations. Since small variations could occur in the environment from one generation to the other, changes in observed variance in the father and son generations could indicate an interaction effect between genotype and environment. Moreover, when similar genotypes or identical randomly selected pools of genes are borne by individuals reared under different experimental environments (as in Experiment II) the unequality of variance for the same variable can provide information concerning the genotype and environment interaction effect.

Behavioral Measures. The rearing conditions and behavioral tests were identical to those described in the first experiment except that the duration of observation for each subject was 15 min. The two variables dealing with swinging (IV and XI) and the four variables dealing with sigmoid display (VII, VIII, IX and X) were measured as defined in Experiment I.

Results and Discussion. Interaction between genotype and environ-

TABLE 4
Comparison of Variances in the Populations of Male Fathers and Male Offspring

	Variables	Father N = 18	Offspring N = 118	F
XIII	Nb. gonopodial swingings	.8816	.8840	1.083 NS
	10 $g_{10(7+x)}$ *			
VI	1/first gonopodial latency	.2991	.3220	1.076 NS
	10 $g_{10(9+x)}$			
VII	Nb. sigmoïds	.0692	.0443	1.562 NS
	10 $g_{10(8+x)}$			
VIII	Duration sigmoïds	.2200	.1992	1.104 NS
	10 $g_{10(9+x)}$			
IX	1/latency first sigmoïd	.2956	.3619	1.224 NS
	10 $g_{10(24+x)}$			
X	Average duration sigmoïds	.0720	.0560	1.285 NS
	10 $g_{10(10+x)}$			

*Transformation.

ment was first tested on the 6 variables. Transformed scores were employed to compare variances: 1) between two successive generations fathers vs. sons; 2) between groups from large vs. small brood and 3) between groups of individuals separated from the brood at 25 vs. 45 days of age. We failed to show an interaction effect between the genotypes and the categories of the environment that we had defined, since none of the *F* values reaches a *p* < .10 level. The estimation of the genetic parameters for the different variables was thus performed (Table 4) admitting that this interaction was negligible but the likelihood of this assumption must be discussed in the light of the other experiments.

The variable XIII. *Nb. gonopodial swingings*, will be considered first (Table 5). The VA/VP ratio is either null (H-S) or nonsignificant (O-OP). Using the first method, the component of the variation attributed to the fathers was negative (−.0003) and thus VA was considered to be zero. This lack of additive variance can be explained by several technical factors: 1) the true variance for number of gonopodial swingings is too small; 2) the inadequacy of the model; 3) the computational method for the components of variation. The first explanation cannot be retained because the reliability of the variables is high (Table 1). The second explanation is not pertinent because it has been demonstrated that the interaction *G* × *E* is not significant. In addition, the sources of variation are independent, the females being randomly affected by males and every male offspring in the litter being observed. The third explanation would

TABLE 5
VA/VP Ratios and Standard Deviations for 6 Variables in Male
Courtship Behaviors Estimated by Regression of Offspring on Father
Value $b_{(O-OP)}$ and Intraclass Correlation of Half Sibs $t_{(H-S)}$

<i>Variables</i>		<i>VA/VP</i> $b_{(O-OP)} \pm SE^*$	<i>VA/VP</i> $t_{(H-S)} \pm SE^*$
XIII	Nb. gonopodial swingings	.18 \pm .78	0
VI	1/first gonopodial latency	0	0
VII	Nb. sigmoïds	.38 \pm .15	.40 \pm .09
VIII	Duration of sigmoïds	.32 \pm .27	.29 \pm .15
IX	1/latency first sigmoïd	.56 \pm .11	.51 \pm .14
X	Average duration sigmoïds	.39 \pm .09	.68 \pm .23

*Computed according to Falconer's method (1963).

suggest that the zero value of the component attributable to males may be the consequence of the computation of causal components by successive subtractions. In fact, the high standard deviation ($.0078 \pm .003$) of the component attributable to the females may have led to a possible overestimation of this component and consequently to an underestimation of the VA. However, the nonsignificant value of VA/VP in the other design where this subtractive computational method is not used, strongly suggests that the number of gonopodial swingings does not have additive genetic correlates in this population. The fact that the variable VI. *1/first gonopodial latency* has a null additive component in the two designs suggests that the conclusion for variable XIII is also true for variable VI.

The two variables VII. *Nb. sigmoïds* and VIII. *Duration sigmoïds* have similar genetic architecture. The component attributed to the females was negative and thus considered to be zero, whereas the VA/VP ratios were in complete agreement in the two designs. For X. *Average duration sigmoïds*, the component attributable to the female differs significantly from zero in the half-sib design. The higher VA/VP ratio in the H-S than in the O-OP design is compatible with an epistatic effect due to linked segregating units, since, as a general rule, the ascendent/descendent covariance is not affected by epistasis when the segregating units are linked, whereas it is affected when computed from full-sib or half-sib designs. The results for X. *Average duration sigmoïds* are compatible with a model including IX. *1/latency first sigmoïd*: the VA/VP ratios do not differ from the O-OP and H-S designs. Moreover, another estimation of the ratio from the O-OP design (Kempthorne & Tandon, 1953) provides a similar value ($.506 \pm .117$). As the component attributable to the females is different from zero, it is possible to consider VA from a full-

sib design. In this case, $VA/VP = .572 \pm .137$, differs from zero and is similar to the other coefficients. This suggests that in this population and for IX. *1/latency first sigmoid* the deviation due to dominance and the common environmental variation that often inflate VA in full-sib designs are null.

The genetic correlations between these variables are reported in Table 6. As a general feature, the agreement is good between the values estimated from the two designs. The variables describing gonopodial swinging (VI and XIII) are not correlated, in spite of their high reliability and good commonalities (see Tables 1 and 2). The correlation between X. *Average duration sigmoïds* and VII. *Nb. sigmoïds* must not be over-emphasized because they are not independent by construction. On the contrary, the common genetic correlates of VIII. *Duration sigmoïds* and VII. *Nb. sigmoïds* should be stressed. The correlations with IX. *1/latency first sigmoid* are either null or weak when compared to their standard deviation. The components of variation and consequently VA/VP and genetic correlation coefficients were estimated here from relatively small samples. An accurate estimation of the coefficient values would need larger samples, but with small populations, indeed, we have demonstrated that the coefficients differ significantly from zero. Moreover, the highly similar estimates obtained from the two independent designs with different populations lend additional weight to the results.

EXPERIMENT IV: DIRECTIONAL SELECTION

When conclusions from biometrical genetics are taken into account, a response to selection is expected for the variables describing sigmoid display and not for variables related to gonopodial swinging.

Material and Methods. The subjects were derived from the heterogeneous population. Over the generations of selection, 565 male guppies served as subjects. The conditions for breeding and observation of behaviors were identical to those presented in the first and third experiments.

Genetic Design. Two behaviors were measured during the test (15 min) and considered for selection: *Nb. gonopodial swingings* as described above and a new variable for sigmoid display: *Incidence of sigmoid display* (presence vs. absence). Individual selections were independently performed in duplicate for the two variables, leading to eight selected lines:

- 1) males exhibiting sigmoid display at least once and labelled S+ and S+';
- 2) males never exhibiting the display: S- and S-';
- 3) males performing the highest number of gonopodial swingings: G+ and G+';

TABLE 6
Sexual Behavior in Male Guppy: Observed Correlations in Parent plus Offspring Males (Under the Diagonal);
Genetic Correlations and Standard Errors (Above the Diagonal), First Line from Half-sib Design; Second Line from
one Parent-offspring Design

	<i>Variables</i>	XIII	VI	VII	VIII	IX	X
XIII	Nb. gonopodial swingings		0	0	0	0	0
VI	1/first gonopodial latency	.40	0	.09 ± .13	.01	0	.01
VII	Nb. sigmoïds	.27	-.02	0	0	0	0
VIII	Duration sigmoïds	.40	.13	.73	.71 ± .12 .86 ± .11	.88 ± .04 .73 ± .10 .31 ± .27 .13 ± .31	-.11 ± .17 -.01 ± .20 0 0
IX	1/latency first sigmoïd	.29	-.04	.16	.64		.11 ± .21 .02 ± .15
X	Average duration sigmoïds	.13	-.07	.57	.41	.18	

4) males performing the lowest number of gonopodial swingings: G- and G-'.

An unselected line bred from the basic population was used as a reference for each of the 8 other lines: UNS.

Twenty percent of the males (either high or low scores) of the observed population were included in each line in each generation. One half was used as progenitors and the sisters of the other half were used for mating. In each line and each generation the numbers of males observed were high enough to yield at least ten male progenitors. The selection was performed over four generations in every line, and was relaxed at generation 3. The continuous variable *N. gonopodial swingings* was analyzed according to an ANOVA procedure. For the dichotomized variable *Incidence of sigmoid display*, the frequencies were compared with a log linear model (Sokal & Rohlf, 1981) and computed with the SAS CATMOD procedure (SAS Institute Inc., 1987); all the main effects and interactions were included in the model.

Results and Discussion

N. gonopodial swingings was considered first. The replicated lines G+ and G+' on the one hand and G- and G-' on the other hand do not differ ($F < 1$ in each comparison). There is no response to selection either for G+ (G+ and G+' being pooled or analyzed separately) or for the G- (the replicated lines being either pooled or independently analyzed) since the generation effect is always comprised between $p < .20$ and $p < .40$. In any case, the selected lines differ from the UNS line (Figure 1).

Incidence of sigmoid display (Figure 2) was then analyzed. Neither S+ and S+' nor the S- and S-' lines differ among each other ($\chi^2_{(1)} = .31$ and 2.14, respectively), so that the replicated lines were pooled. The S+ and S- generally differ ($\chi^2_{(1)} = 74.49$) and the difference is increased with the number of generations ($\chi^2_{(3)} = 13.84$ for the interaction between lines and generation). The difference reaches the $p < .05$ level as soon as generation 1 and remains significant for generations 2 and 4. The relaxation of the selection at the 3rd generation does not modify the difference between the lines. The upper line S+ differs from the UNS line ($\chi^2_{(1)} = 74.49$) but the difference is acquired at the first generation and remains constant at the 2nd and 3rd generations. The lower line also differs from the UNS line ($\chi^2_{(1)} = 24.23$) but the $p < .05$ significance level is only reached at the second generation. The reduction of the incidence of sigmoid display across the generations reaches the $p < .003$ value ($\chi^2_{(3)} = 12.64$). Generally, there is no asymmetry between the S+ and S- lines when each of them is compared to the UNS. The *Incidence of sigmoid display* is no more than a dichotomization of *Nb. sigmoids* and the observed response to selection for this variable is in agreement

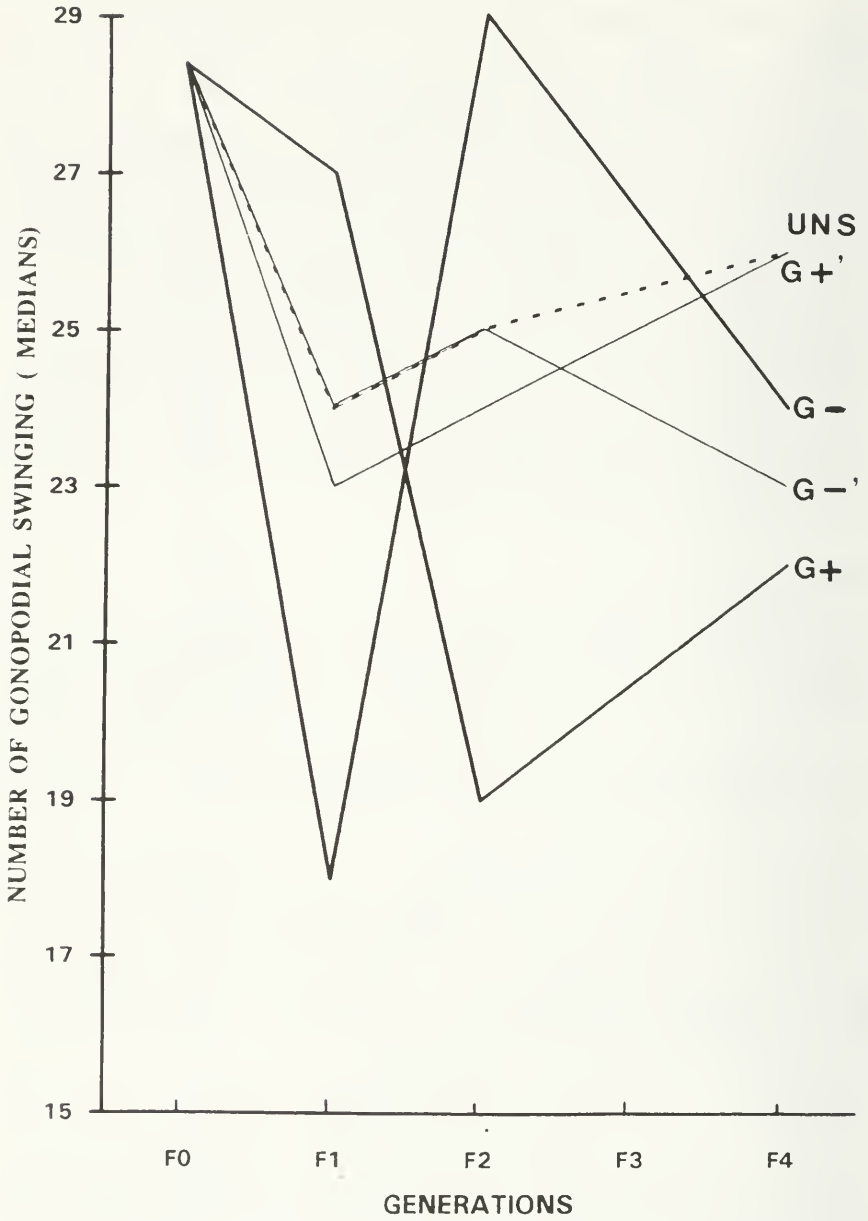


FIGURE 1. Response to selection for the number of gonopodial swingings (selection relaxed at generation 3); see the text for the abbreviations.

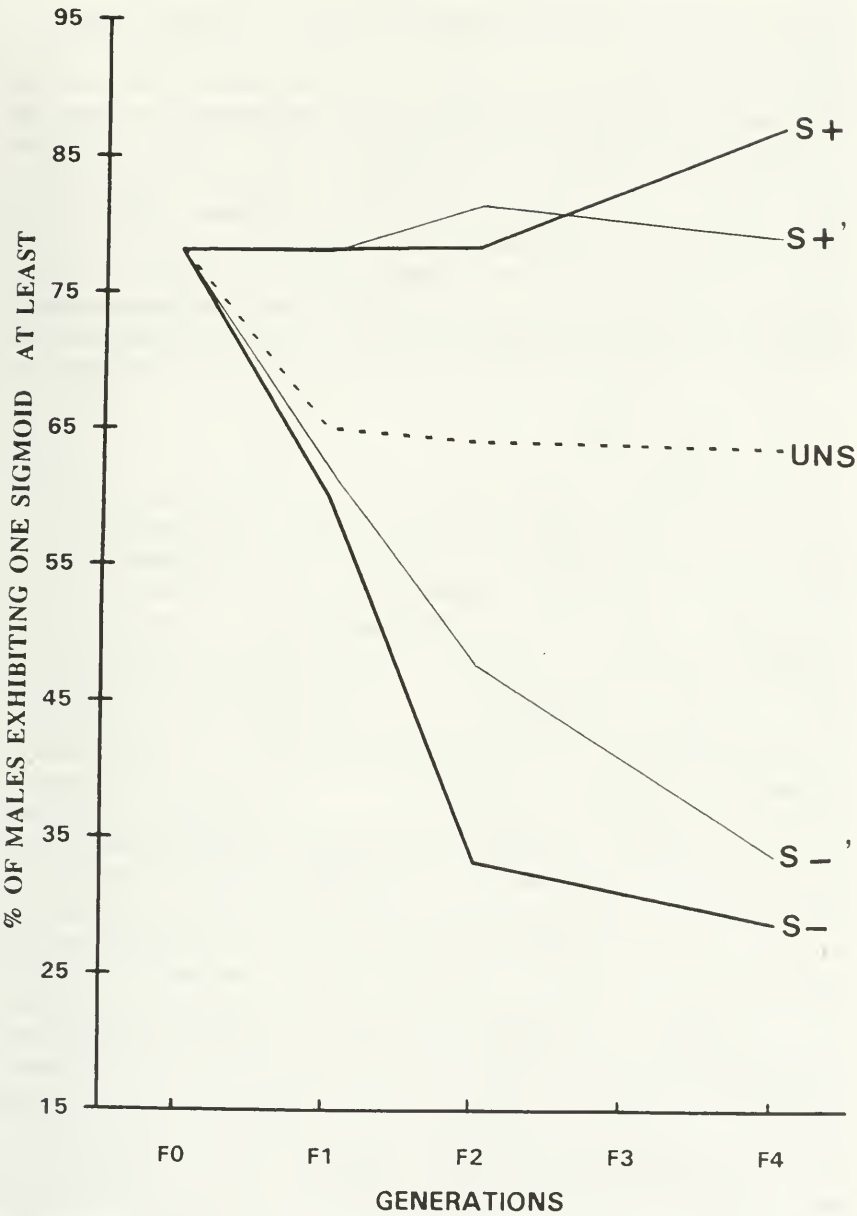


FIGURE 2. Response to selection for the presence vs. absence of sigmoid display (selection relaxed at generation 3); see the text for the abbreviations.

with the significant VA/VP values obtained from the quantitative genetic analyses.

The correlated responses to selection were examined for the variables considered in Experiment III. There is obviously no correlated response for the *Nb. gonopodial swingings*. The S+ and S- lines were then considered. In the S+ line *Average duration sigmoïds* is higher ($F = 5.83$) and *1/latency first sigmoïd* shorter ($F = 7.85$) than in the S-. The correlated responses to selection reveal a structure of the observed sexual behavior in the male guppy that is compatible with the conclusion drawn from the quantitative genetic analysis. The measures of the gonopodial swingings and sigmoïd display appear to be genetically independent whereas in this last group the variables have common additive correlates.

GENERAL DISCUSSION

Individual differences were observed for variables measured during a standardized test for sexual behavior in male *Poecilia reticulata*. The factorial structure of individual differences is stable. A general factor appears and the second factor allows two categories of behavior to be distinguished. The first deals with gonopodial swinging and attempt to copulate, the second with characteristics of the species-specific display called "sigmoïd." The quantitative genetic analysis (with both male offspring-father and half-sibs designs) leads to an additive estimate for the variables employed to measure gonopodial swinging which is not significantly different from zero. On the contrary, most of the variables related to sigmoïd display have additive components that differ significantly from zero in the two designs. The conclusions from the directional selection experiment are those expected from the estimated values of the quantitative genetic analysis. We were not able to obtain a response for the number of gonopodial swingings whereas selected responses in duplicate were effective both for absence and presence of sigmoïd display (presence vs. absence). This agreement confirms the fitness of the biometrical models we have employed and the fact that the data were compatible with the requirements for these models. The test for an interaction between genotype and environment raises particular problems with these models and this species. The nonsignificant value found by the test we had employed for this source of variation is supported by both the agreement of the quantitative genetic estimates with the results of the selection and by the similar range of variation within each line for each generation.

The lack of additive variance for the variables used to measure the characteristics of gonopodial swinging and our failure to obtain a response to any selection does not exclude the contribution of other sources of genetic variation that are undetectable with the available methods. The absence of detectable additive genetic correlates for the measures of

gonopodial swingings could be interpreted according to two hypotheses. First, it would be the consequence of the natural selection pressure for the trait, having an obvious functional usefulness for the survival of the species. It could be considered as being fixed, the allelic forms correlated with the unadaptive low number of gonopodial swingings having been eliminated. Second, the variation observed for the variables VI and XIII could only have environmental correlates. We have no evidence favoring the first hypothesis deduced from the synthetic evolution dogma. On the other hand, the high reliability, found for these variables, confirms that their observed variations are not random, but correspond to stable individual characteristics. The values reached by these coefficients and the high loadings in the factorial analysis indicate the large margin of their true variations. Moreover, we have demonstrated the susceptibility of variable XIII. *Nb. gonopodial swingings* to the effects of early environment but other sources of early environmental modifications could also be efficient as suggested by Laming and Loughin (1987).

The most surprising conclusion deals with the measures of sigmoïd display, a species-specific characteristic of this behavior (that is not found in other *Poecilidae* (Liley, 1966)). We could thus expect a null genetic additive variation as a consequence of a selection against the genotypes correlated with low frequencies of the display. This is not the case here, as confirmed both by quantitative genetic analysis and selection. Unfortunately, the biological material and subsequently the biometrical models available for their analysis did not provide the means to test for other genetic components. The symmetry in the S+ and S- lines does not lead to the suggestion of a dominance effect. Moreover, a directional dominance hypothesis with the effect of recessive alleles associated with the reduction of sigmoïd display can be eliminated; it would not fit with the absence of inbreeding depression that we had found for frequency of sigmoïd behavior (Roubertoux, unpublished). But the hypothesis of directional gene frequencies cannot be excluded since this only has effects on long term selection and would not be detectable at the fourth generation. The significant additive genetic source of variation, the only source proven at present in this research, could be interpreted in two ways. First, it could be an indicator of a weak adaptive value of this species-specific trait, the sigmoïd display, thus leading to cautious interpretations of behavior-genetic analysis in evolutionary perspectives. Second, the result of a possible stabilizing selection could be invoked to explain the genetic additive variability underlying sigmoïd behavior.

The differences between the conclusions from an analysis of the observed and genetic correlations is not surprising since the first are the results of genetic and environmental covariations and of their interactions (Hirsch, 1967, who points out the misinterpretations of correlational conclusions). The observed correlations between gonopodial swinging and sigmoïd measurements are not due to genetic factors but to envi-

ronmental ones. The sexual behavior pattern appears to be composed of sequences, some of them being heritable, but the coordination of these sequences has environmental correlates. This fact prevents any simple link between additive genetic variance and evolution as far as species-specific behaviors are considered.

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